

Differential sensitivities of grassland structural components to changes in precipitation mediate productivity response in a desert ecosystem

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Summary

1. In arid and semi-arid ecosystems, there are legacies of previous-year precipitation on current-year above-ground net primary production. We hypothesized that legacies of past precipitation occur through changes in tiller density, stolon density, tiller growth, axillary bud density and percentage of viable axillary buds. We examined the sensitivity to current- and previous-year precipitation of these grassland structural components in *Bouteloua eriopoda*, the dominant grass in the northern Chihuahuan Desert.

2. We conducted a rainfall manipulation experiment consisting in –80% reduced precipitation, ambient, +80% increased precipitation treatments that were subjected to one of five precipitation levels in the previous two years (–80% and –50% reduced precipitation, ambient, +50% and +80% increased precipitation). The first two years preconditioned the experimental plots for year three, in which we created wet-to-dry and dry-to-wet transitions. Measurements were taken in year 3.

3. We found that stolon density was the most sensitive to changes in precipitation and that percent-active buds were insensitive.

4. We also found that past precipitation had a significant legacy on grassland structural components regardless of the precipitation received in the current year, and that the legacy occurs mostly through changes in stolon density.

5. Here, we showed that there is a differential sensitivity of structural components to current and past precipitation and supported previous findings that vegetation structure is one of the controls of productivity during precipitation transitions.

Key-words: axillary buds, *Bouteloua eriopoda*, desert grassland, meristem bank, precipitation legacies, vegetative reproduction

Introduction

Above-ground net primary production (ANPP) of a grassland ecosystem, which is expressed in $\text{g m}^{-2} \text{ year}^{-1}$, is the result of the growth of each individual shoot and the density of these shoots. The latter, in turn, depends on the vegetative recruitment from the population of meristems and thus the fraction of meristems that is active and not dormant. This phenomenon by which the population of meristems controls primary production is also known as meristem limitation (Geber 1990). This point of view con-

trasts with the ecosystem approach that suggests that grassland ANPP is most frequently controlled by water availability (Noy-Meir 1973; Sala *et al.* 1988). These two approaches without a doubt complement each other. In other words, water availability directly affects ANPP through changes in C fixation at the leaf level and indirectly through changes in ecosystem structure, which, in grasslands, includes the density of individual plants, their identity and the density of tillers.

Water availability is the most frequent limiting factor of the functioning of arid and semi-arid ecosystems (Noy-Meir 1973). Ecologists have documented strong spatial relationships between mean annual precipitation and mean ANPP across precipitation gradients for different regions

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The loss in immediate production is balanced by the plants long-term persistence in a variable environment, allowing the plant to survive after disturbance or stress (Bloom, Chapin & Mooney 1985). We tested two hypotheses linking vegetation structure dynamics to precipitation: (i) dormant, active meristem, tiller and stolon density will have different sensitivities to precipitation; with a hierarchy of responses based on theories of resource allocation strategies for growth and storage (Bloom, Chapin & Mooney 1985). We predict that tiller growth will show the highest precipitation sensitivity, followed by the density of tillers and stolons, the percentage of active buds per tiller and lastly the number total axillary buds per tiller. (ii) There will be a legacy of past precipitation on grassland structural components, and legacies would have a greater effect on production of buds than on investments with instantaneous-profit-like tiller growth.

We tested our hypotheses by decreasing or increasing rainfall for two years and a reversed treatment in year 3 where some plots under drought during years 1 and 2 were irrigated and some under wet conditions in years 1 and 2 were subjected to drought. We assessed the effects on ANPP and dormant, active meristem, tiller and stolon density in *Bouteloua eriopoda* (Torr.) Torr. (black grama).

Materials and methods

EXPERIMENTAL DESIGN

The study was conducted at the Jornada Basin Long Term Ecological Research site (32.5°N, 106.8°W, 1188 m.a.s.l.) located in the northern Chihuahuan Desert, NM. Mean annual precipitation from 1915–1995 was 245 mm, and average temperature was 14.7 °C. Vegetation type is desert grassland dominated by *Bouteloua eriopoda* (black grama) and *Prosopis glandulosa* Torr. (honey mesquite). Soils are coarse-textured, well-drained, sandy loams soils (Typic Paleothids; Soil-Survey-Staff 1999), with a layer of calcium carbonate found at depths from 64–76 cm. (Herbel, Ares & Wright 1972; Gibbens *et al.* 1986).

The rainfall manipulation consisted of 5 levels of precipitation (P) from 2007–2009 (20%, 50%, 100%, 150% and 180% of natural ambient). During year 3, the treatments were reversed so plots that had previously received drought (20 and 50%) in year 3 either stay the same or received irrigation. Similarly, plots that in years 1 and 2 received irrigation, in year 3 either stay the same or received drought. We used 2.5 × 2.5 m plots with an $N = 6$ and doubled number of replicates in control yielding a 66 total number of plots. This experimental design generated plots that had the same precipitation treatment for three years and plots that had dry/wet and wet/dry precipitation transitions in 2009, each treatment with six replicates. Response variables were measured once at the end of 2009 growing season, with the exemption of axillary buds per tiller and percentage of active axillary buds that were also measured before the 2009 growing season started. Ambient water-year precipitation was 344 mm in 2007, 312 mm in 2008 and 118 mm in 2009.

We installed individual rainout shelters in reduced-precipitation plots (Yahdjian & Sala 2002). Shelters had 2 levels of rainfall reduction of 50 and 80% achieved using different numbers of transparent acrylic 'shingles' per shelter. Precipitation reduction was achieved by reducing the total amount without modifying the natural precipitation pattern. Shingles were transparent, molded

from acrylic ACRYLITE® FF, a material with high light transmission (>92% PAR transmitted) and less than 3% change in light transmission over a 10-year period (CYRO Industries, Parsippany, NJ, USA). Previous tests on this type of rainout shelter showed that their effects on light and temperature were minimal (Yahdjian & Sala 2002). Rainout shelters were left in place throughout the duration of the experiment and only removed to perform measurements.

For the water addition treatments, we installed an irrigation system to water the plots with sprinklers. We watered the plots with an extra 50% or 80% of each precipitation event greater than 2 mm using rainfall collected off-site. Due to a drier-than-average growing season during 2009, wet treatments received 5 additional irrigation events of 20 mm each in September.

RESPONSE VARIABLES

Above-ground net primary production. We used non-destructive annual measurements of vegetation cover and site-specific cover-to-biomass regressions to estimate black grama ANPP. Regressions of plant cover vs. live biomass were obtained by double sampling cover and biomass (Flombaum & Sala 2007). The data set to construct the cover–biomass relationship consisted of forty 20 × 100 cm plots where we measured black grama cover and harvested the grass at peak growing season. Plant cover was evaluated with two parallel lines per plot, where we recorded green and standing dead interception per species present in the plot. We obtained a regression of black grama biomass (g m^{-2}) = $264.56 * \text{black grama per cent cover}$, $N = 20$, $r^2 = 0.68$, $p < 0.001$. Grass cover ranged between 0.09 and 0.80 percentage. The regression was forced through zero (Flombaum & Sala 2007) because zero biomass yields zero productivity. We measured plant cover with three parallel lines in each treatment plot, each of 250 cm length and evenly spaced from the east border. We recorded green interception per species for all plants present in the plot and used the regressions to obtain an estimate of biomass by species. Annual above-ground net primary production of black grama was equated to green biomass at peak biomass (Sala & Austin 2000; Flombaum & Sala 2007) in 2009.

Tiller and stolon density. We counted the number of physiologically active tillers and stolons of black grama at peak biomass in 2009. Tillers were counted within permanent 40-cm diameter rings and scaled up to a square metre area. Rings were located in a black grama patch representative of the plot. Stolons were counted if they belonged to tillers within the ring. Physiologically active tillers and stolons were those with at least one green leaf present at the moment of sampling.

Production per tiller. Production per tiller, or tiller growth, was calculated as the ratio between black grama ANPP for 2009 and tiller density in 2009.

Total axillary buds and percentage of active axillary buds per tiller. We harvest 2 or 3 black grama crowns per plot in the fall of 2009 (mid-October, end of growing season). We also collected crown samples in the spring of 2009 to detect any possible difference in the response of viable buds to phenology (Ott & Hartnett 2011). We examined bud viability and total axillary buds per tiller under a dissecting microscope within two weeks from harvest. Samples were washed free of soil, and ten to fifteen tillers were picked haphazardly, totalling 900 to 1400 tillers per sampling date. We incubated the base of tillers in darkness at 30 °C for 15 h in 0.6% (m/v) 2,3,5-Triphenyl Tetrazolium Chloride (TTC) solution, as described in Busso, Mueller & Richards (1989). Enzymatic activity reduces TTC to an insoluble red formazan, showing red, metabolically active buds under the dissecting scope. We calculated the percentage of active axillary buds from the total bud population and the number of axillary buds per tiller.

STATISTICAL ANALYSES

We used mixed linear models to test the effects of precipitation and previous-year precipitation on each response variable (proc mixed procedure, SAS® 9.2, SAS Institute Inc., Cary, NC, USA). First, we fitted least square linear regressions to examine how each response variable responded to changes in precipitation. This analysis only included results from plots that always had the same precipitation treatment throughout the experiment. Block effect was included in all the analyses as a random effect, and the REML method (Restricted or Residual Maximum Likelihood) was used to calculate the variance component, which produces smaller estimates for the random effects. For the purpose of this study, we defined annual precipitation as the water-year precipitation received between October 1 and September 30. We calculated water-year precipitation input per precipitation treatment by either adding the irrigated amount or by subtracting the percentage intercepted by rainout shelters to the ambient precipitation. The second part of the analyses consisted of determining the sensitivity of different response variables to current- and previous-year precipitation. Sensitivity analysis was performed by comparing standardized slopes of each response variable to changes in precipitation. Standardization consisted of calculating a new response variable, the natural logarithm of the response ratio, $\ln(R_i) = \ln(X_{ij}/\bar{X}_{ic})$, where X_{ij} is the observed quantity for variable i in the experimental plot j , and \bar{X}_{ic} is the mean response of i variable in ambient precipitation plots. The ratio R is a unit-less measure of the experimental effect, as it quantifies the relative change of each variable that results from the manipulation. We used the natural logarithm of R because its sampling distribution is more normal than that of R (Hedges, Gurevitch & Curtis 1999). Next, we used a mixed model to describe the relationship among the response ratio $\ln(R)$, the i classification variables, the covariate precipitation and the experimental units. Given that all response variables were measured in the same experimental units, we added a plot within block repeated statement to account for the covariance structure of the data (Littell *et al.* 2006). Differences in precipitation sensitivity

were tested with the equal slope hypothesis and pairwise comparisons among slopes. Sensitivity to precipitation legacies was studied with a similar mixed model that included two covariates, P_t and P_{t-1} , and we tested whether previous year precipitation had a significant effect on the response once that the effect of current-year precipitation was accounted for. Precipitation was treated as a continuous variable. We report whole model R^2 and p values for individual effect tests.

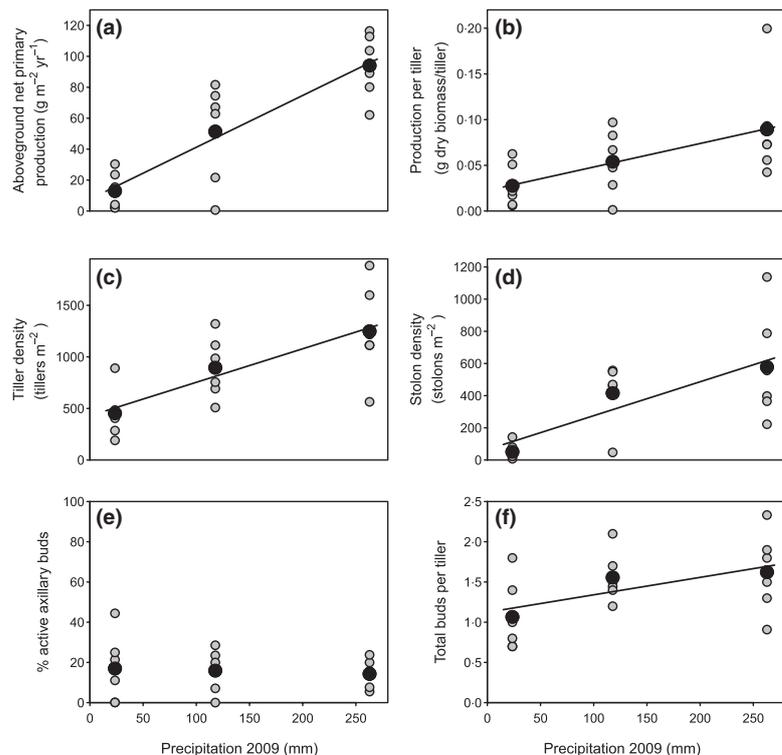
Results

ANPP AND COMPONENTS OF ECOSYSTEM STRUCTURE RESPONSES TO CHANGES IN PRECIPITATION

There was a significant, positive linear relationship between black grama ANPP and water-year precipitation (Fig. 2a) that explained 89% of the variation in ANPP for 2009 ($\text{ANPP}_{2009} \text{ g dry biomass m}^{-2} \text{ year}^{-1} = 7.69 + 0.33 P \text{ (mm)}$, $p < 0.0001$, $n = 18$). Production per tiller also increased with increasing precipitation in year 2009 (Fig. 2b). Precipitation explained 53% of the variation in 2009 production per tiller ($\text{production/tiller}_{2009} \text{ g dry biomass tiller}^{-1} = 0.0224 + 0.00026 P$, $p = 0.0075$, $n = 18$).

Black grama tiller and stolon density measured at the end of the growing season increased linearly with precipitation received during 2009 (Fig. 2c-d). Mean tiller density in irrigated plots was almost three-fold greater than in drought plots ($\text{Tillers m}_{2009}^{-2} = 428.50 + 3.25 P_{09}$, $p < 0.001$, $R^2 = 0.50$, $n = 18$). Stolon densities increased by 500% in irrigated compared to drought treatments during 2009 ($\text{Stolons m}_{2009}^{-2} = 64.61 + 2.11 P$, $p = 0.0015$, $R^2 = 0.48$, $n = 18$). Our result of tiller density in the natural ambient

Fig. 2. Effect of water-year precipitation on above-ground net primary production (a), production per tiller (b), tiller density (c), stolon density (d), per cent active axillary buds (e) and total axillary buds per tiller (f) in 2009. All response variables increased with increasing precipitation (P) except for the percentage of active axillary buds that was insensitive to changes in precipitation. Grey dots represent experimental unit's response. Black dots represent the mean response variable per precipitation level. Lines represent significant linear relationships. $\text{ANPP}_{2009} \text{ g dry biomass m}^{-2} \text{ year}^{-1} = 7.69 + 0.33 P \text{ (mm)}$, $R^2 = 0.89$, $p < 0.0001$, $n = 18$; $\text{production/tiller}_{2009} \text{ g dry biomass tiller}^{-1} = 0.0224 + 0.00026 P$, $R^2 = 0.53$, $p = 0.0075$, $n = 18$. $\text{Tillers m}_{2009}^{-2} = 428.50 + 3.25 P_{09}$, $p < 0.001$, $R^2 = 0.50$, $n = 18$; $\text{Stolons m}_{2009}^{-2} = 64.61 + 2.11 P$, $p = 0.0015$, $R^2 = 0.48$, $n = 18$; % active buds $\text{buds}_{\text{fall}2009} = 17.31 \pm 4.74$, $R^2 = 0.01$, $p = 0.7$, $n = 18$; Axillary buds $\text{tiller}_{\text{fall}2009}^{-1} = 1.12 + 0.022 P$, $p = 0.05$, $R^2 = 0.21$, $n = 18$.



precipitation treatment of 1600 tillers m^{-2} was comparable to stem densities found by Dalglish & Hartnett (2006; Littell *et al.* 2006) in an experimental site in northern New Mexico.

The percentage of active axillary buds did not respond to incoming precipitation (Fig. 2e, $p = 0.7$). About 20% of axillary buds were active in the fall of 2009. In the spring, before the onset of the growing season, 40% of buds were active on average, and this was not related to precipitation either (results not shown). The number of total axillary buds per tiller found in the fall increased with precipitation (Axillary buds tiller $_{fall2009}^{-1} = 1.12 + 0.022 P$, $p = 0.05$, $R^2 = 0.21$, $n = 18$), and the magnitude of the change (~35%) was similar to the increase in axillary buds with precipitation in the spring (Axillary buds tiller $_{sp2009}^{-1} = 1.54 + 0.002 P$, $p = 0.003$, $R^2 = 0.25$, $n = 32$; Fig. 2f). The proportion of viable buds and axillary buds numbers of 1 to 3 per tiller found in *Bouteloua eriopoda* were comparable with previous studies on *B. curtipendula* (Hendrickson & Briske 1997) and *Stipa spp.* (Flemmer, Busso & Fernandez 2002).

SENSITIVITY OF THE COMPONENTS OF ECOSYSTEM STRUCTURE TO CURRENT- AND PREVIOUS-YEAR PRECIPITATION

All response variables except percentage of active buds were affected by changes in current-year precipitation, but some were more sensitive than others (Fig. 3). There are two important results from this analysis. First, sensitivity to precipitation was, in all cases, positive, because all response variables increased with increasing precipitation. Secondly, stolon density was the most sensitive to changes

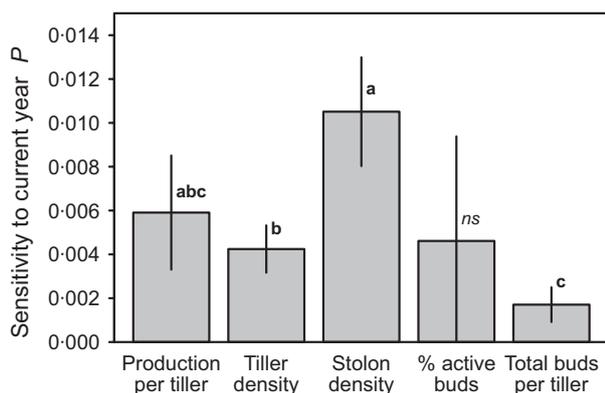


Fig. 3. Sensitivity of ecosystem structure components to changes in current water-year precipitation. Stolon density was the most sensitive to changes in precipitation (P), followed by production per tiller and tiller density. The variable total axillary buds per tiller was the least sensitive component to changes in precipitation and % of active axillary buds did not change with precipitation. For each component of the meristem bank, sensitivity is the slope estimate (± 1 ES) for the precipitation effect in a mixed model of the natural logarithm of the response ratio, with meristem bank components as fixed effect, precipitation as covariate and plot within block as repeated statement. Different letters represent significant differences among sensitivities (a–b difference $p = 0.005$; b–c difference $p = 0.08$; a–c difference $p = 0.003$).

in current-year precipitation, followed by production per tiller, tiller density and total buds per tiller.

Previous-year precipitation had a significant effect on tiller density, stolon density and axillary buds per tiller (Fig. 4). Stolon density was the most sensitive to *previous-year precipitation*, followed by tiller density and total buds per tiller. Production per tiller and % of active buds were not sensitive to previous-year precipitation. Regardless of current-year precipitation, plots with previous dry conditions had fewer tillers, stolons and axillary buds than plots with a wet history. Different components of population structure had a similar hierarchy of response to legacies of previous-year precipitation than to current-year precipitation (Figs 3 and 4).

Discussion

Our study supported the hypothesis that different components of the ecosystem structure had different sensitivities to precipitation (Fig. 3). Stolon density, production per tiller and tiller density were the most affected by precipitation. The number of stolons was the most sensitive structural component to changes in precipitation and stolon growth has been proposed to be the principal regeneration process in black grama (Nelson 1934). Why does stolon population change more than tiller population in response to more precipitation? Stoloniferous expansion is a reproductive strategy that allows the daughter plant to establish further away from the parent plant than by tillering, and to establish in an open patch with less competitive pressure. In arid ecosystems such as the Chihuahuan Desert grassland, there are large patches of bare soil in between grass tussocks. Therefore, we speculate that

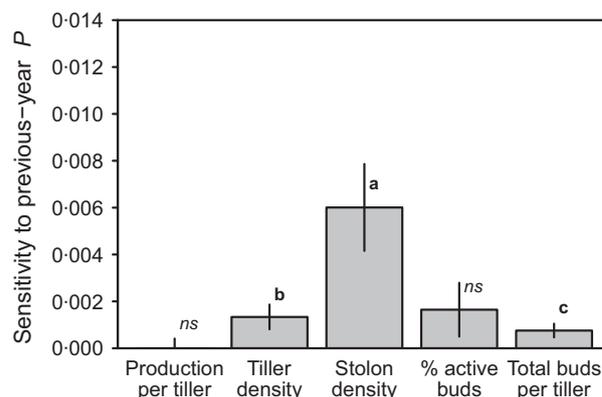


Fig. 4. Sensitivity of ecosystem structure components of previous-year precipitation. Stolon density was the most sensitive to precipitation (P) legacies, followed by tiller density and total axillary buds per tiller. For each component of the meristem bank, sensitivity is the slope estimate (± 1 ES) for the effect of previous-year P (P_{t-1}) in a mixed model of the natural logarithm of the response ratio, with meristem bank components as fixed effect, P and P_{t-1} as covariates and plot within block as repeated statement. Different letters represent significant differences among sensitivities (a–b difference $p = 0.014$; a–c difference $p < 0.0001$; b–c difference $p = 0.003$).

horizontal expansion of grass tussocks is much more advantageous from the standpoint of acquiring resources than growing new tillers adjacent to the mother plant. Expansion predominantly through stolons may hold for arid grasslands where competition for below-ground resources is dominant but probably will not hold for mesic grasslands driven by light competition.

Contrary to our prediction, total percentage of active buds was not sensitive to precipitation. Plants have anticipating mechanisms that are controlled by external stimuli, like changes in the photoperiod or temperature (Casal, Sanchez & Deregibus 1986). Plants that respond to environmental cues before the onset of water or temperature stress may have a competitive advantage relative to those that respond directly to stress (Casal, Sanchez & Deregibus 1986; Shimizu-Sato & Mori 2001). Regulated by plant hormones like auxin and cytokinin, a low-maintenance axillary bud bank reserve might break dormancy as a response mechanism to biomass loss resulting from either herbivory, fire or drought (Lehtilä 2000; Shimizu-Sato & Mori 2001). Therefore, it is likely that bud dormancy is controlled by cues other than precipitation.

The axillary bud density was sensitive to precipitation in contrast to what has been reported for other grass species (Flemmer, Busso & Fernandez 2002), with consequences on the population of active buds. Previous evidence suggested that the number of axillary buds produced in each tiller was an inflexible trait (Hendrickson & Briske 1997). Our results were different from those of Flemmer, Busso & Fernandez (2002) who found that the number of total axillary buds per tiller was insensitive to precipitation in perennial tussock grasses from South America. We speculate that the difference between our results and those reported previously is associated with the strength of the experimental manipulation. In our case, the experimental precipitation change was $\pm 80\%$. In Flemmer's case $+70\%$ and -10% in year 1, and $\pm 10\%$ in year 2. In synthesis, the number of axillary buds may be sensitive to changes in water availability, but this effect becomes evident only under severe alterations of water availability. At the tiller level, the number of active buds depends both on the percentage of active buds ($\sim 20\%$, Fig. 2e) and the total number of buds/tiller that increased with increasing precipitation (Fig. 2f). Thus, changes in precipitation indirectly affect the population of active axillary buds by unit area by changing the density of total axillary buds in tillers and tiller density.

Our study suggests that changes in black grama ANPP in response to changes in precipitation occur mostly through changes in stolon and tiller number and the amount they grow. Although stolons and tillers have a similar structure (Langer 1972), they have different functions in the plant. Tillers were three times more abundant than stolons and account for most of the photosynthetic biomass. We hypothesize that increased water availability first stimulates production per tiller (highest marginal profit) until it reaches a maximum. At this point, changes in ANPP only occur through changes in tiller density.

Sensitivity to previous-year precipitation was lower than sensitivity to current-year precipitation but was still significant. We hypothesize that the effect of precipitation on the different structural components decreases as the window of observation becomes larger. In other words, sensitivity of structural components to current-year precipitation is higher than sensitivity to previous year that is higher (we speculate) than sensitivity to precipitation of the previous two years. The precipitation effect gets diluted through time.

One implication of this study on the understanding of ecosystem functioning is the notion that precipitation imposes legacies on the vegetation structure. Lauenroth & Sala (1992) hypothesized that the temporal controls of productivity respond to slow changes in vegetation structure. Here, we showed that past precipitation affects current-year tiller populations and supported previous findings that vegetation structure provides feedbacks on productivity to precipitation transitions (Reichmann, Sala & Peters 2013).

Results from our work highlight the importance of meristem dynamics and vegetation structure in controlling ecosystem functioning. Interactions between population and ecosystem phenomena are growing in recognition from the studies of biodiversity on ecosystem functioning of the last decade to the recently recognized importance of meristem abundance from tillers to seeds, in fostering conservation efforts (Kettle *et al.* 2011).

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