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

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Summary

1. In arid and semiarid ecosystems, there are legacies of previous-year precipitation on current-year aboveground net primary production. We hypothesized that legacies of past precipitation occur through changes in tiller density, stolon density, tiller growth, axillary bud density and percent 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 done in year 3.
3. We found that stolon density was the most sensitive to changes in precipitation and that percent-active buds was 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

Meristem bank, axillary buds, precipitation legacies, desert grassland, vegetative reproduction, *Bouteloua eriopoda*

Introduction

Aboveground net primary production (ANPP) of a grassland ecosystem, which is expressed in g m^{-2} yr^{-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 contrasts 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 semiarid ecosystems (Noy-Meir 1973). Ecologists have documented strong spatial relationships between mean annual precipitation and mean ANPP across precipitation gradients for different regions around the world (Sala *et al.* 1988; McNaughton, Sala & Oesterheld 1993; Jobbágy, Sala & Paruelo 2002; Bai *et al.* 2008; Sala *et al.* 2012). Temporal productivity-precipitation relationships for individual sites are far weaker than spatial relationships, and account for only 20 to 40% of the interannual ANPP variability (Lauenroth & Sala 1992; Briggs & Knapp 1995;

64 Jobbágy & Sala 2000; Hsu, Powell & Adler 2012; Sala *et al.* 2012). This low explanatory power
65 of temporal precipitation patterns results from legacies of previous-year precipitation on current-
66 year ANPP, reducing current-year production when the previous year was drier than the current
67 and enhancing it when the previous year was wetter (Sala *et al.* 2012; Reichmann, Sala & Peters
68 2013). In the Chihuahuan desert, nearly 40% of legacy variability results from changes in
69 previous-year tiller density (Reichmann *et al.* 2013), revealing that the indirect effect of past
70 precipitation on ANPP occurs through changes in vegetation structure. ANPP was higher when
71 the previous year was wetter than when the previous year was drier relative to current year; and
72 an important fraction of ANPP variation was explained by tiller density.
73 We propose a framework that combines ecosystem ecology with population ecology to
74 understand ecosystem-level processes (Figure 1). Under this framework, precipitation directly
75 and indirectly affects ANPP. Ecosystem ecologists have extensively studied the direct effect of
76 resource availability on ecosystem functioning (Sala *et al.* 1988; Huxman *et al.* 2004). The
77 indirect effect occurs through population and community level processes mediating the ANPP
78 response. Tiller recruitment and sexual reproduction are the mechanisms that allow plant and
79 population persistence in perennial grasslands. In some arid-semiarid ecosystems, successful
80 establishment from seeds is rare, representing in some cases less than 1% of total aboveground
81 stems (Nelson 1934; Neilson 1986; Lauenroth *et al.* 1994; Rogers & Hartnett 2001). Thus,
82 population persistence of perennial grasses is shaped by meristem limitation as grasses rely upon
83 the vegetative recruitment from the population of meristems. The bud-bank (sensu Harper 1977)
84 is the primal source for tillers and functions like a seed bank; but unlike seeds that may outlast
85 their parent plants, the presence of buds in a bud bank depends on living individuals. Similar to
86 seeds, these buds have innate or induced dormancy, and the activation or breaking of dormancy

is an obligated step in vegetative regeneration (Klimesova & Klimes 2007). The density of tillers or stolons depends on the density of buds and the fraction that is activated (Figure 1). Factors affecting meristem density have impacts on the maintenance of relative species abundance (Busso, Mueller & Richards 1989; Hendrickson & Briske 1997; Laterra, Deregibus & Maceira 1997; Benson, Hartnett & Mann 2004). For example, grazing may affect grass persistence by increasing the proportion of dead axillary buds per tiller (Flemmer, Busso & Fernandez 2002) or by reducing tiller density (Becker *et al.* 1997; Wan & Sosebee 2002). The effect of resource availability on axillary bud density, activation, and tiller recruitment and its consequences for ecosystem functioning has received relatively small attention in the literature (but see Busso *et al.* 1989; Dalgleish *et al.* 2008; Dalgleish & Hartnett 2009).

This paper aims at answering a central question of the relationship between precipitation variability and ecosystem structure in grassland ecosystems. How do growth per tiller, tiller density, bud density and percent bud dormancy respond to current and previous-year precipitation? Grassland structural components with high sensitivity to changes in precipitation, i.e. those that exhibit the highest relative change to changes in precipitation, would be the most important for mediating the effects of precipitation on ANPP. Theory predicts that plants invest in current-year growth and produce new leaves rather than investing in organs that will sustain future growth until the marginal revenue from the increased production is equal to the marginal cost (Bloom, Chapin & Mooney 1985). Investing in organs that will sustain future growth occurs at a minimal cost but it will come last, because it results in a diversion of resources from growth. 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 *et al.* 1985). We tested two hypotheses linking vegetation structure dynamics to precipitation: 1) 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 *et al.* 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. 2) 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 asl) 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 X 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). 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

Aboveground 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 x 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 * black grama percent cover, N=20, r^2 = 0.68, $p < 0.001$. Grass cover ranged between 0.09 and 0.80 percent. 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 aboveground 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-meter area. Rings were located in a black grama patch representative of the plot. Stolons were counted if they belonged to tillers within the ring.

179 Physiologically active tillers and stolons were those with at least one green leaf present at the
180 moment of sampling.
181 **Production per tiller,** or tiller growth, was calculated as the ratio between black grama ANPP
182 for 2009 and tiller density in 2009.
183 **Total axillary buds and percent active axillary buds per tiller.** We harvest 2 or 3 black grama
184 crowns per plot in the fall of 2009 (mid-October, end of growing season). We also collected
185 crown samples in the spring of 2009 to detect any possible difference in the response of viable
186 buds to phenology (Ott & Hartnett 2011). We examined bud viability and total axillary buds per
187 tiller under a dissecting microscope within two weeks from harvest. Samples were washed free
188 of soil and ten to fifteen tillers were picked haphazardly, totaling 900 to 1400 tillers per sampling
189 date. We incubated the base of tillers in darkness at 30ºC for 15h in 0.6 % (m/v) 2.3.5-Triphenyl
190 Tetrazolium Chloride (TTC) solution, as described in Busso *et al.* (1989). Enzymatic activity
191 reduces TTC to an insoluble red formazan, showing red, metabolically active buds under the
192 dissecting scope. We calculated the percent of active axillary buds from the total bud population
193 and the number of axillary buds per tiller.
194
195 *Statistical Analyses*
196 We used mixed linear models to test the effects of precipitation and previous-year
197 precipitation on each response variable (proc mixed procedure, SAS® 9.2, SAS Institute Inc.).
198 First, we fitted least square linear regressions to examine how each response variable responded
199 to changes in precipitation. This analysis only included results from plots that always had the
200 same precipitation treatment throughout the experiment. Block effect was included in all the
201 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 1st and September 30th. 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, $\ln(R_i) = \ln(X_{ij}/\overline{X}_{ic})$, where X_{ij} is the observed quantity for variable *i* in the experimental plot *j*, and $\overline{X}_{ic}$ 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 (Figure 2 a) that explained 89% of the variation in ANPP for 2009 ($ANPP_{2009}$ g dry biomass m^{-2} yr^{-1} = 7.69 + 0.33 *P* (mm), $p < 0.0001$, n=18). Production per tiller also increased with increasing precipitation in year 2009 (Figure 2 b). Precipitation explained 53% of the variation in 2009 production per tiller (production/$tiller_{2009}$ 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 (Figures 2 c and d). Mean tiller density in irrigated plots was almost three-fold greater than in drought plots (Tillers $m^{-2}{}_{2009}$= 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 (Stolons $m^{-2}{}_{2009}$= 64.61 + 2.11 *P*, $p = 0.0015$, R^2 = 0.48, n=18). Our result of tiller density in the natural ambient precipitation treatment of 1600 tillers m^{-2} was comparable to stem densities found by Dalgleish and 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 (Figure 2 e, 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 $tiller^{-1}_{fall2009}$=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 $tiller^{-1}_{sp2009}$ =1.54 +0.002 *P*, p = 0.003, R^2 = 0.25, n=32) (Figure 2 f). 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 *et al.* 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 (Figure 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. Second, stolon density was the most sensitive to changes 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 (Figure 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 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 (Figures 3 and 4).

Discussion

Our study supported the hypothesis that different components of the ecosystem structure had different sensitivities to precipitation (Figure 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 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 belowground resources is dominant but probably will not hold for mesic grasslands driven by light competition.

Contrary to our prediction, total percent 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 *et al.* 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.

293 The axillary bud density was sensitive to precipitation in contrast to what has been
294 reported for other grass species (Flemmer *et al.* 2002), with consequences on the population of
295 active buds. Previous evidence suggested that the number of axillary buds produced in each tiller
296 was an inflexible trait (Hendrickson & Briske 1997). Our results were different from those of
297 Flemmer et al. (2002) who found that the number of total axillary buds per tiller was insensitive
298 to precipitation in perennial tussock grasses from South America. We speculate that the
299 difference between our results and those reported previously is associated with the strength of the
300 experimental manipulation. In our case, the experimental precipitation change was ± 80%. In
301 Flemmer's case +70% and -10% in year 1, and ± 10% in year 2. In synthesis, the number of
302 axillary buds may be sensitive to changes in water availability but this effect becomes evident
303 only under severe alterations of water availability. At the tiller level, the number of active buds
304 depends both on the percentage of active buds (~20 %, Figure 2 e) and the total number of
305 buds/tiller that increased with increasing precipitation (Figure 2 f). Thus, changes in precipitation
306 indirectly affect the population of active axillary buds by unit area by changing the density of
307 total axillary buds in tillers and tiller density.
308 Our study suggests that changes in black grama ANPP in response to changes in
309 precipitation occur mostly through changes in stolon and tiller number and the amount they
310 grow. Although stolons and tillers have a similar structure (Langer 1972), they have different
311 functions in the plant. Tillers were three times more abundant than stolons and account for most
312 of the photosynthetic biomass. We hypothesize that increased water availability first stimulates
313 production per tiller (highest marginal profit) until it reaches a maximum. At this point, changes
314 in ANPP only occur through changes in tiller density.

Sensitivity to previous-year precipitation was lower than sensitivity to current 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 and 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 *et al.* 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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454

Figures

Figure 1. Conceptual diagram of the effects of precipitation on the different components of vegetation structure and their interactions (modified from Ott & Hartnett 2012). Precipitation affects aboveground net primary production (ANPP) both directly and indirectly by affecting the bud bank size, active buds, tiller and stolon recruitment, growth and death. Precipitation that occurred in the previous-year affects ANPP indirectly through tiller retention and resource storage into buds, with possible downstream effects.

Figure 2. Effect of water-year precipitation on aboveground net primary production (a), production per tiller (b), tiller density (c), stolon density (d), percent 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. Gray dots represent experimental units response. Black dots represent the mean response variable per precipitation level ± 1 SE. Lines represent significant linear relationships. $ANPP_{2009}$ g dry biomass m^{-2} yr^{-1} = 7.69 + 0.33 *P* (mm), R^2= 0.89, p < 0.0001, n=18;; production/$tiller_{2009}$ g dry biomass $tiller^{-1}$ = 0.0224+0.00026 *P*, R^2 =0.53, p = 0.0075, n=18. Tillers $m^{-2}{}_{2009}$= 428.50 + 3.25 P_{09}, *p* < 0.001. R^2 = 0.50, n=18; Stolons $m^{-2}{}_{2009}$= 64.61 + 2.11 *P*, *p* = 0.0015, R^2 = 0.48, n=18; % active buds $_{fall2009}$ = 17.31 ± 4.74, R^2= 0.01, p = 0.7, n=18; Axillary buds $tiller^{-1}{}_{fall2009}$=1.12+0.022 *P*, *p* = 0.05, R^2 = 0.21, n=18.

Figure 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).

Figure 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).

494 *Figure 1*

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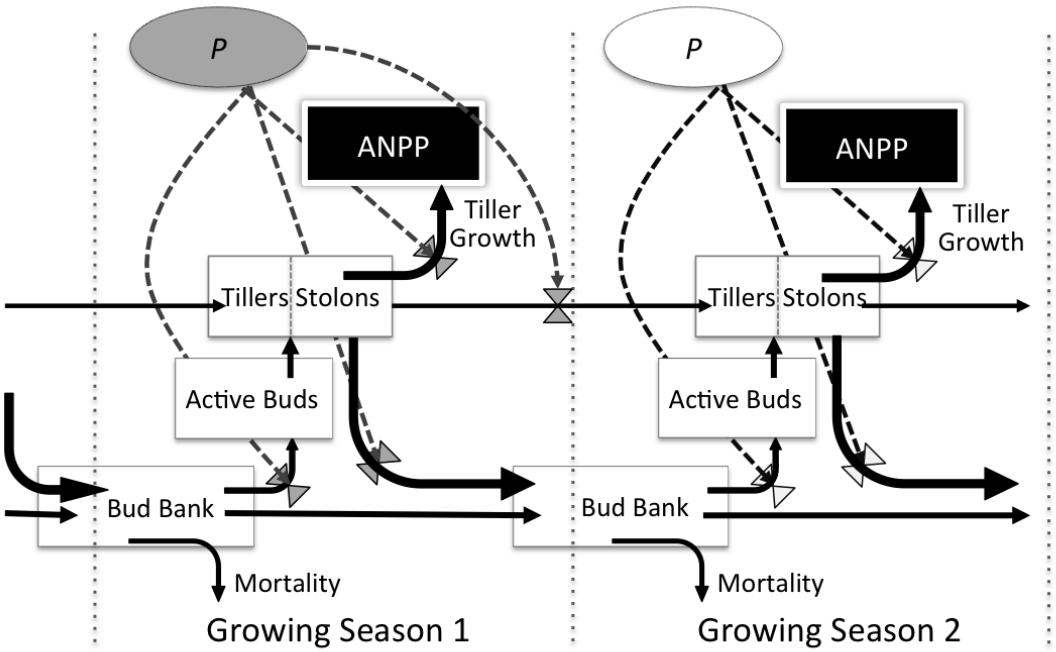

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497 *Figure 2*

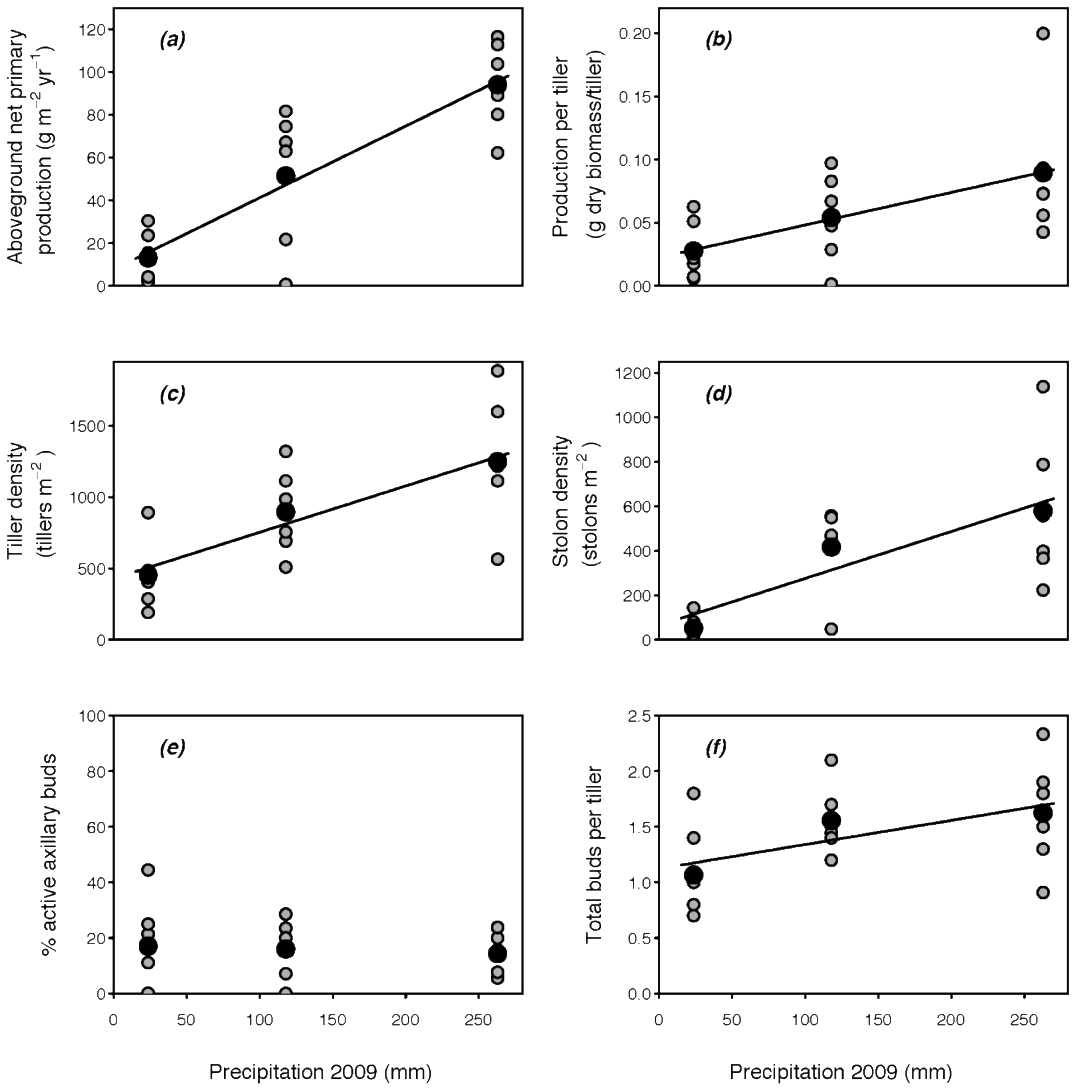

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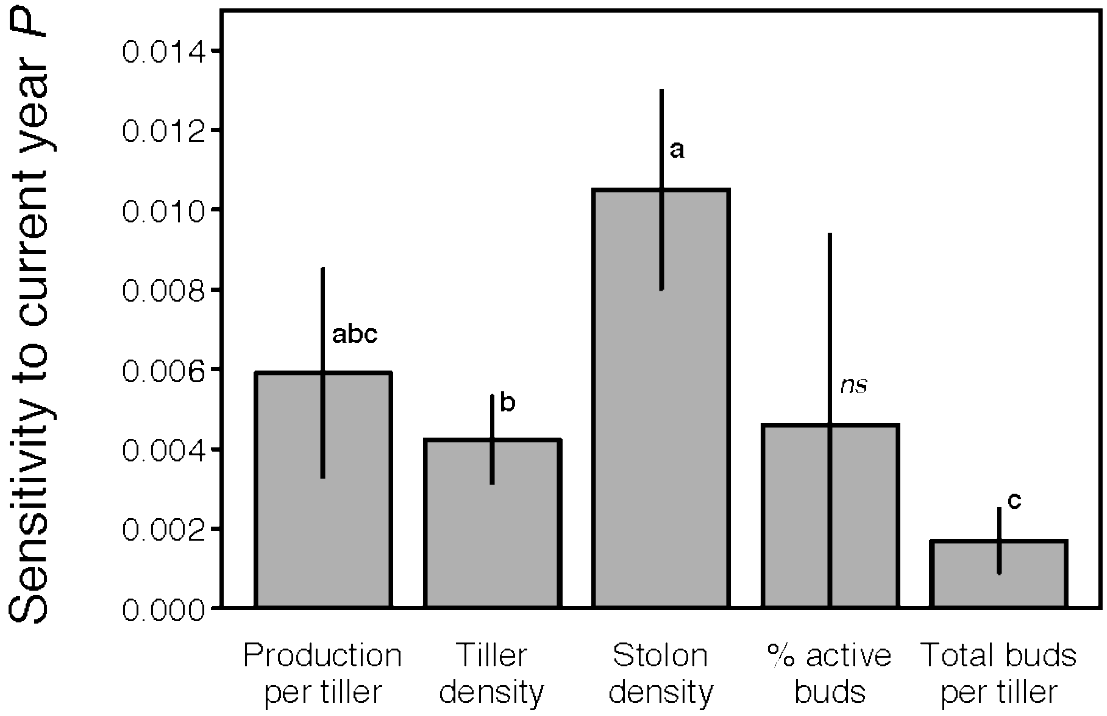
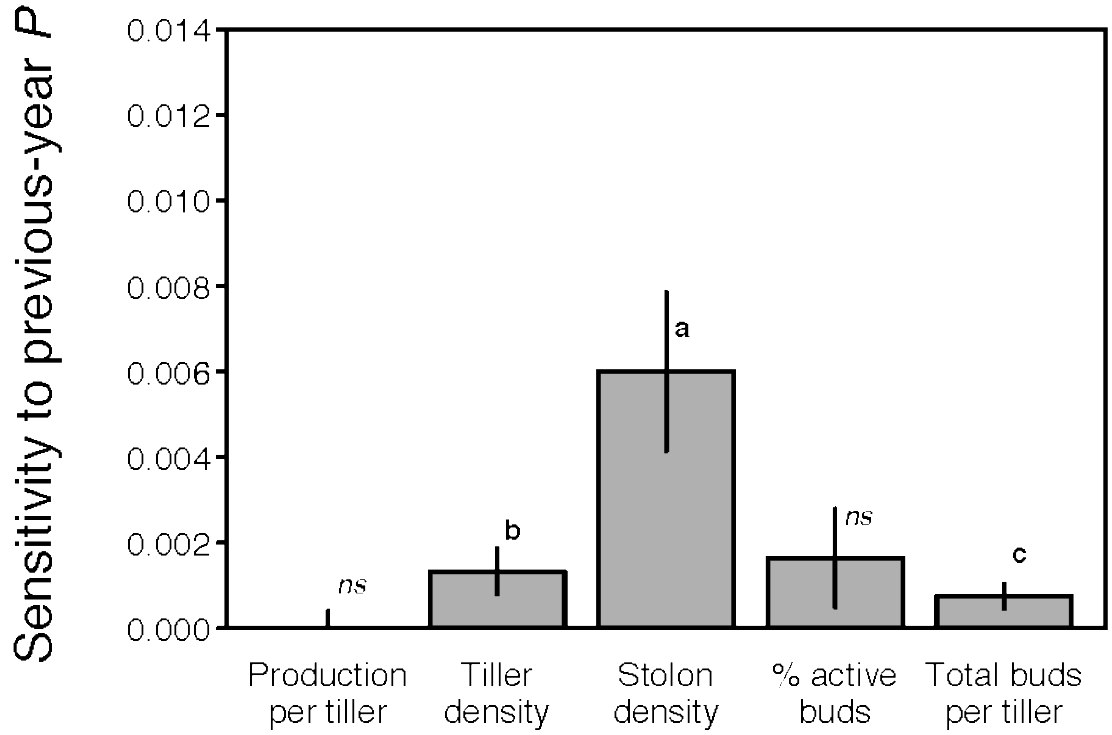
Figure 3


Sensitivity to current year P
0.014
0.012
0.010
0.008
0.006
0.004
0.002
0.000
abc
b
a
ns
c
Production per tiller
Tiller density
Stolon density
% active buds
Total buds per tiller

503 *Figure 4*



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