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Simulating diverse native C_4 perennial grasses with varying rainfall

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ABSTRACT

Rainfall is recognized as a major factor affecting the rate of plant growth development. The impact of changes in amount and variability of rainfall on growth and production of different forage grasses needs to be quantified to determine how climate change can impact rangelands. Comparative studies to evaluate the growth of several perennial forage species at different rainfall rates will provide useful information by identifying forage management strategies under various rainfall scenarios. In this study, the combination of rainfall changes and soil types on the plant growth of 10 perennial forage species was investigated with both the experimental methods, using rainout shelters, and with the numerical methods using the plant growth simulation model, ALMANAC. Overall, most species significantly increased basal diameter and height as rainfall increased. Like measured volume, simulated yields for all species generally increased as rainfall increased. But, large volume and yield increases were only observed between 350 and 850 mm/yr. Simulating all species growing together competing agrees relatively well with observed plant volumes at low rainfall treatment, while simulating all species growing separately was slightly biased towards overestimation on low rainfall effect. Both simulations agree relatively well with observed plant volume at high rainfall treatment.

1. Introduction

Climate change will significantly affect water resources through changes in rainfall rates and increases in extreme events such as drought. Over the last two decades, the U.S. has seen an increase in average annual rainfall, but there are regional differences, with some areas having increases and others having decreases (Melillo et al., 2014). According to the IPCC (2007), more rain is expected in the equatorial belt (humid tropics) and at higher latitudes, whereas less rain is expected in mid-latitudes, semiarid areas, and the dry tropics. As the spatial extent and severity of drought increases (Dai, 2010), the frequency of short-term drought is expected to double, and long-term drought will become three times more common in regions with less rainfall (Sheffield and Wood, 2008). This extreme variability in rainfall will have diverse effects on soil moisture availability and consequently, forage production and quality (Rötter and Van de Geijn, 1999). Forty percent of variation in annual forage production is associated with annual precipitation over a wide range of areas (Lauenroth and Sala, 1992). Therefore, a better understanding of the impacts of changing rainfall change on forage production will ideally translate into reduced enterprise risk and more efficient forage production through increased predictive capacity to improve management decisions with expected climate change.

Many studies have focused on the relationship between rainfall and forage production with varying thoroughness using several forage grass types (Nelson, 1934; Paulsen and Ares, 1962; Cable, 1975; Knapp et al., 2006; Derner and Hart, 2007; Miranda et al., 2011; Hou et al., 2013; Chaplin-Kramer and George, 2013). Forage species show various growth and production patterns in different rainfall patterns and amounts because of differences in their vegetative and root structures. According to Barker and Caradus (2001), at low rainfall status (high soil moisture deficit), it is preferable for the plant to have low green leaf area to minimize leaf water loss and heating from radiation. For example, highly drought-tolerant forage species such as blue grama and black grama have lower leaf area index (LAI) at high water deficit (Kiniry et al., 2002). These prairie grasses are able to survive and grow in drier soils and in more drought-prone regions (Leithead et al., 1976;

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Schleicher and Anderson, 2007; Lloyd-Reilley and Masher, 2011; Tober and Jensen, 2013). Gherardi and Sala (2015) also reported that shrubs, described as long-lived perennial plants with deep root systems, showed increasing production with increasing precipitation variability. In contrast, the production of dominant grasses, described as short-lived perennial grasses with shallow root systems, decreased forage yield with increasing precipitation variability. According to these results, growth and production patterns vary among plant species under different rainfall patterns. Thus, comparative studies evaluating growth of diverse perennial forage grass species at different rainfall rates will provide useful information that helps producers estimate annual forage production at different rainfall rates and better understand growth of perennial grasses.

In this study, the effect of rainfall on growth of ten perennial forage grass species was investigated both by experimentally varying rainfall using a rainout shelter and with the plant growth simulation model ALMANAC (Kiniry et al., 1992). Because soil texture can have a major role in modifying the spatial and temporal availability of water to plants (Bristow et al., 1984; Smith et al., 1995; Schlesinger and Pilmanis, 1998; Sperry et al., 1998; Hacke et al., 2000), the field experiment was carried out in two different soil textures (clay, and mixture of clay and sandy soils). The objectives of this study were to (i) evaluate grass responses to various rainfall rates in terms of plant volume and plant stand structure (basal diameter and height); (ii) determine the dependence of those responses on soil texture; and (iii) determine how reasonably ALMANAC simulates grass production under these rainfall rates.

2. Materials and methods

2.1. Plant materials

Ten perennial forage species were included in this study (Table 1). Purple three-awn (*Arisida pupurea*) is a bunchgrass with densely turfed culms that is commonly found in dry coarse or sandy soils in desert valley (Tilley and John, 2013). Three *Bouteloua* species, sideoats grama (*Bouteloua curtiperdula*), black grama (*Bericopoda ericopoda*), and blue grama (*Bouteloua gracilis*), were used in this study. Sideoats grama is a deep rooted bunchy or sod-forming grass that is adapted to a broad range of sandy to clayey textured soils (Wynia, 2007). Black grama is a tufted grass with wiry, woolly culms that grows mostly on dry gravelly or sandy soils (Magee, 2016). Blue grama is a bunchgrass commonly found on the plains, prairies, and foothills and grows well on soil types that are sandy to clayey in texture (Wynia, 2007). Hall's panicum (*Panicum hallii*) is an erect turf grass grown on sandy to clayey calcareous soils (Lloyd-Reilley and Masher, 2011). Big bluestem (*Andropogon gerardii*) is a tall bunchgrass that is well adapted to moist, well-drained sandy and clay loam soils (Owsley, 2011). Little bluestem (*Schizachyrium scoparium*) is a bunchgrass with culms slightly flattened and is also well adapted to sandy and clay loam soils (Tober and Jensen, 2013). Switchgrass (*Panicum virgutum*) upland type is a tall bunch grass and grows well on moderately deep to deep, somewhat dry to poorly drained, sandy to clay loam soils (Carter, 2011). Indiangrass (*Sorghastrum nutans*) is a tall bunchgrass and grows well in deep, well drained floodplain soils, and in well drained upland sandy loam soils (Owsley, 2011). Tall dropseed (*Sporoloulus coupsitus*) is a bunchgrass well adapted to deep clay soils that are intermittently wet and dry (Magee, 2005).

Seeds of the ten species were purchased from Native American Seed (Junction, TX) or provided by the University of Texas at Austin Lady Bird Johnson Wildflower Center Seed Bank (Table 1). The seeds were germinated and grown in seedling trays on field soils under ambient greenhouse conditions for 12 weeks before transplanting into field plots on August 19, 2010. After transplanting, the plants were established and maintained by watering 2–3 times per week at 1000 mm/yr before rainfall treatments began. No data were collected in 2011. Rainfall treatments were imposed on May 22, 2012.

Table 1
Identification of plant materials used in this study.

Scientific name	Common name	Origin
Aristida purpurea	Purple three-awn	Native American Seed
Bouteloua curtipendula	Sideoats grama	Native American Seed
Bouteloua eriopoda	Black grama	Native American Seed
Bouteloua gracilis	Blue grama	Native American Seed
Panicum hallii	Hall's panicum	Wildflower Center Seed Bank
Andropogon gerardii	Big bluestem	Native American Seed
Schizachyrium scoparium	Little bluestem	Native American Seed
Panicum virgatum	Switchgrass	Native American Seed
Sorghastrum nutans	Indiangrass	Native American Seed
Sporoloulus compositus	Tall dropseed	Wildflower Center Seed Bank

2.2. Experimental design

The plant growth experiment was conducted in rainout shelter plots from 2012 to 2014. The rainout shelter is located at the Lady Bird Johnson Wildflower Center of The University of Texas at Austin in Texas, U.S. (Fig. 1A). The experiment was laid out in a split plot based on a randomized completed block design with four replications. Rainfall treatment was considered as the main plot and two soil types were treated as subplots. To avoid high competition for water and light, 10 forage grass species were divided into two communities based on plant size: shortgrass and tallgrass. The shortgrass community included purple three-awn, black grama, blue grama, Hall's panicum, and sideoat grama; the tallgrass community included big bluestem, little bluestem, indiangrass, tall dropseed, and switchgrass. Shortgrass and tallgrass communities were planted on same replicate plot and were treated by every unique treatment combination. In each replicate plot, 3 individuals of each species were planted, in a grid with 0.5 m spacing. Positions were assigned in a stratified random design and repeated across all replicate plots. Three rainfall treatments (350 mm/yr, 850 mm/yr, and 1331 mm/yr) were selected based on the driest, average, and wettest ten years in the historical record for Austin, TX (Fig. 1B). The rain treatment applications were created using a stochastic weather generator, LARS-WG 5.5 (Semenov et al., 1998), which was calibrated using an 87-year precipitation record. The rainfall sequences approximated the historic mean amount, seasonality, size distribution, and spacing of rainfall events. Two soil types were used in this experiment: clay and a mix of clay with sand. Clay soil was collected from the local area (Speck stony clay loam), and rocks greater than 50 mm in diameter were sieved out. The clay-sand mix was local clay soil mixed 3:1 with 99.7% silica sand mesh size with 5 mm openings.

2.3. Plant measurements

Plant sizes were measured annually in July 2012–2014. To estimate total plant volume, we measured the maximum basal diameter, basal diameter perpendicular to the maximum basal diameter, and plant height. Plant height was measured from the ground to the top of the tallestleaf. Basal diameter was calculated by averaging the two measured basal diameters. Plant volume was calculated assuming the plant was a cone. This consisted of multiplying the basal surface area by the plant height, and then dividing the outcome by 3. Basal area was calculated by multiplying

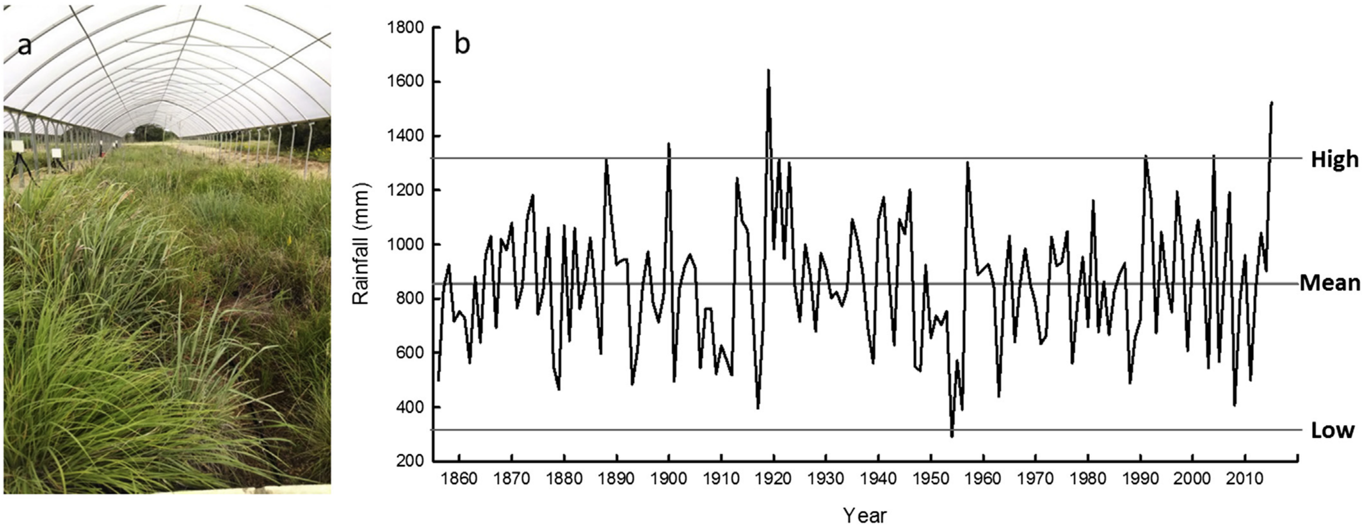

Fig. 1. (A) Photographs of rain shelter and (B) mean annual rainfall between 1856 and 2015 in Austin.

two basal radii and pi (π). Values of leaf area index (LAI) for all species were obtained from the ALMANAC model database (Kiniry et al., 1992).

2.4. Model evaluation

The ALMANAC model (Kiniry et al., 1992) was used to simulate plant yield at different rainfall rates. We ran the simulation in Travis County, Texas, on Speck stony clay loam soil. Soil information was downloaded from the USDA NRCS SSURGO database: http://websoilsurvey.nrcs.usda.gov/. (Accessed 09/15/2015). Soil depth, wilting point, and field capacity were changed to closely resemble conditions at our field site. Depth was changed from 0.51 m to 0.23 m. Attempts to simulate the soil with the sand amendment did not show different grass yields. Thus only the simulated results for the local clay soil were reported. The relative responses of plant volume (measured) were compared to the relative responses for dry matter (simulated). In each case the low irrigation treatment was compared to the mean irrigation treatment and the high irrigation treatment was compared to the mean treatment. Measured volumes were the mean for both soils. Management inputs included planting species from seed in normal conditions three years prior to applying irrigation treatments. Hence, species would be established before the field treatments began. Simulations were approached from two different perspectives. In the first, each grass species was simulated separately. In the second, species were simulated competing within each community. For this last simulation, the five shortgrasses were planted in the same area, one day apart, and the same strategy was used for the tallgrasses. Thus competition experienced in the field site was simulated by the model. In order to insure no nutrient limitations occurred in the simulations, and because initial soil fertility was unknown, fertilizer was applied at 50 kg/ha nitrogen and P_2O_5 on the first day of April, May, June, and July each year in the simulations. Weather from National Oceanic and Atmospheric Administration (NOAA) (NOAA, 2012) was used in the simulation, but precipitation was set to zero. We used the mean solar radiation near Austin, TX (NOAA, 1993) reducing it to 85% of the original values to account for light attenuation by the rainout shelter. Plots in establishment years were irrigated every seven days from February 1st to August 30th with 25 mm of water to ensure optimal growth. A harvest was taken every year on October 30th. Irrigation treatments began in 2012, the fourth year of the simulation. The same management schedule was kept, but now the irrigation per treatment was adjusted. For each weekly application, 7 mm of water was applied for the low irrigation, 18 mm for the mean irrigation, and 28 mm for the high irrigation. The irrigation treatments were imposed for 3 years, representing the same years in which the shelters were measured (2012–2014).

ALMANAC contained parameters for all but three of the species (purple three-awn, tall dropseed, and Hall's panicum). In the individual species model simulations, potential LAI was representative of these species in this planting pattern. For purple three-awn, we used big bluestem as a template and changed the DMLA (maximum potential leaf area index) to 5.8 and the HMX (maximum potential height) to 0.5 m. Tall dropseed used little bluestem as a template and changed the DMLA to 2.65 and the HMX to 0.6 m. Hall's panicum used blue grama for its template, and we changed the DMLA to 1.85 and the HMX to 0.6 m. Potential heat units for every species were set to 1800 with a base temperature of 12 °C (Kiniry et al., 2002). For the plant competition runs, the potential LAI of each species was set to approximately 1/6 of the potential LAI of the previous runs. This took into account that six species were originally planted in the field site. One species from each group died out before the conclusion of the experiment, and therefore was not included in this paper. However, each species listed still only occupied 1/6 of the plot area.

2.5. Statistical analysis

The effects of rainfall, soil type, and species and their interaction effects on basal diameter and plant height were analyzed with repeated measures analysis of variance (RMANOVA) with 95% confidence limits using Statistical Analysis Software version 9.3 (SAS Institute., NC, USA). Year was considered as the repeated measure. The rainfall treatment, soil type, and species were considered as fixed effects. The general linear model (GLM) analysis and Fisher's protected least significant difference (LSD) test were conducted within each soil type for each species to test significant differences among rainfall treatment rates for basal diameter and plant height ($\alpha = 0.05$).

3. Results and discussion

Plant stand structure, including basal diameter and height of ten forage grass species, responded differently to rainfall treatments

($P = 0.0004$ and $P < 0.0001$, Table 2). There was also a significant interaction between rainfall treatment and species, indicating that species responded differently to rainfall treatments. The basal diameter and plant height of most of species, except for sideoats grama, Hall's panicum, and little bluestem, increased as rainfall increased (Table 3). Similar results have been observed in short prairie grasses (e.g., blue grama) (Nelson, 1934; Smoliak, 1956) and Great Plains tall prairie grasses (e.g. switchgrass, big bluestem, and indiangrass) (Hartman et al., 2012; Avolio and Smith, 2013; Weatherford and Myster, 2011). For sideoats grama, Hall's panicum, and little bluestem, the lack of response to rainfall treatments might be due to their high tolerance to water stress (Weaver and Albertson, 1956; Wynia, 2007; Tober and Jensen, 2013; Lloyd-Reilley and Masher, 2011).

Soil type also had an effect on grass basal diameter ($P = 0.0055$), with grasses expanding more in the clay-sand soil than in clay soil (Table 3). This might be due to a slower spread of roots in clay soils or differences in soil water availability. A similar result was observed in mesquite trees (*Prosopis glandulosa*), which increased their abundance at a greater rate on sandy upland soils (Medina, 1996). However, many soil responses have depended on species or rainfall. The response of plant height to soil type differed by species ($P < 0.0001$), with switchgrass and indiangrass growing better in the mixed clay-sand soils. There was an effect of the rainfall by soil type by species interaction on basal diameter, indicating that each grass on different soil types responded differently to rainfall ($P = 0.0138$). Basal diameter of purple three awn, black grama, big bluestem, and indiangrass significantly increased as rainfall increased in the mixed clay-sand soils, but not when grown in clay soils (Table 2). Basal diameter of switchgrass was significantly affected by rainfall when it grew in clay soils (Table 2).

Plant species differed in basal diameter and height (both $P < 0.0001$, Table 2), which was reflected in differences in volume among species (Fig. 2). Switchgrass was the largest grass among the ten species, whereas black grama, blue grama, and Hall's panicum were the smallest.

Moreover, plant volume was highly positively correlated with leaf area index (LAI) (Table 4). As plant size increased, the LAI generally increased (Fig. 2 and Table 4). The LAI, defined by leaf area per unit of ground area, is a critical factor controlling water flux by plants between the terrestrial biosphere and the atmosphere. According to previous studies (Waring, 1983; Schlesinger and Pilmanis, 1998; Barker and Caradus, 2001; Kiniry et al., 2013), rainfall variation significantly affecting water availability in soil has been related to the plant canopy LAI. In this study, different potential values of LAI were used for each species in between monoculture and competition simulating runs. According to Kiniry et al. (2002), the potential LAI for sideoats grama was changed based on level of stresses such as nutrient deficiency and drought. The short grasses such as purple three-awn, black grama, blue grama, Hall's panicum, and sideoats grama had potential LAI values in the monoculture runs of 0.7–2.5 and 0.1 to 0.4 for the competition runs. Tall grasses such as big bluestem, little bluestem, indiangrass, tall dropseed, and switchgrass were grown together and the potential LAI values in the monoculture runs were 2.5–6.8 and 0.5–1.1 for the competition runs (Table 4).

Table 2
ANOVA significant tests for main effects and interactions of basal diameter and plant height on ten species used in this study ($P < 0.05$). We use "n.s." to indicate no significant difference.

Source	Basal diamater		Plant height	
	df	*P-Value*	df	*P-Value*
Rainfall (R)	2	0.0004	2	<0.0001
Soil (S)	1	0.0055	1	n.s.
R x S	2	n.s.	2	n.s.
Species (SP)	9	<0.0001	9	<0.0001
R x SP	18	0.016	18	0.0082
S x SP	9	n.s.	9	<0.0001
R x S x SP	18	0.0138	18	n.s.

Table 3
Means of plant crown diameter and height over 3 years under different soil types and rainfall treatment rates for the ten grass species used in this study. Means with same letters are not significantly different within each soil type and each species for rainfall treatment rate ($P < 0.05$; ANOVA, LSD).

Plant	Soil	Basal diameter (cm)			Plant height (cm)		
		Annual precipitation (mm)			Annual precipitation (mm)		
		326	850	1331	326	850	1331
Purple three-awn	Clay	21^{a}	18^{a}	22^{a}	37^{b}	50^{a}	50^{a}
	Clay&Sand	18^{b}	23^{a}	20^{ab}	41^{b}	51^{a}	47^{a}
Sideoats grama	Clay	22^{a}	25^{a}	24^{a}	46^{a}	50^{a}	52^{a}
	Clay&Sand	28^{a}	24^{a}	23^{a}	49^{a}	47^{a}	49^{a}
Black grama	Clay	10^{a}	11^{a}	13^{a}	27^{a}	28^{a}	34^{a}
	Clay&Sand	10^{b}	14^{a}	13^{ab}	23^{b}	25^{b}	35^{a}
Blue grama	Clay	16^{a}	16^{a}	16^{a}	26^{b}	34^{a}	35^{a}
	Clay&Sand	15^{a}	14^{a}	15^{a}	27^{b}	31^{b}	37^{a}
Hall's panicum	Clay	8^{a}	9^{a}	11^{a}	29^{a}	29^{a}	35^{a}
	Clay&Sand	13^{a}	16^{a}	11^{a}	43^{a}	42^{a}	34^{a}
Big bluestem	Clay	15^{a}	18^{a}	15^{a}	61^{a}	68^{a}	73^{a}
	Clay&Sand	11^{b}	18^{a}	23^{a}	45^{c}	59^{b}	80^{a}
Little bluestem	Clay	18^{a}	17^{a}	21^{a}	40^{a}	48^{a}	43^{a}
	Clay&Sand	21^{a}	19^{a}	17^{a}	36^{a}	43^{a}	39^{a}
Switchgrass (upland)	Clay	27^{b}	38^{a}	35^{a}	69^{b}	92^{a}	92^{a}
	Clay&Sand	37^{a}	39^{a}	41^{a}	79^{b}	98^{a}	102^{a}
Indiangrass	Clay	28^{a}	26^{a}	24^{a}	52^{b}	66^{a}	62^{ab}
	Clay&Sand	25^{b}	29^{ab}	32^{a}	47^{b}	69^{a}	80^{a}
Tall dropseed	Clay	17^{a}	19^{a}	17^{a}	45^{b}	56^{a}	55^{a}
	Clay&Sand	15^{a}	16^{a}	19^{a}	49^{a}	57^{a}	52^{a}

In general, simulated yield of prairie forage grass species increased as rainfall increased (Table 4). A similar result was reported by Kiniry et al. (1999) who reported that plant yields significantly increased with precipitation, shown as the maximum yields were observed in sideoats grama, big bluestem, and switchgrass at high precipitation. However, the increases in yield were particularly pronounced between 350 mm/yr and 850 mm/yr (Table 4). This result reveals that these plants growing under the rainout shelter condition could produce yields close to their maximum yields at 850 mm/yr precipitation.

Plant volume and biomass are highly correlated ($R = 0.86$) (Proulx et al., 2015), so relative changes in measured plant volume were compared to relative changes in simulated yield (Table 5). When simulating each species separately, the model generally overestimated the impact of the low irrigation treatment relative to the mean treatment, while doing a somewhat better job simulating the high irrigation treatment relative to the mean (Table 5). For shortgrasses, the mean of measured volume for the low irrigation was 64% of mean of the measured volume at mean irrigation, while mean of the simulated yield for the low irrigation was 40%. For the tallgrasses, mean of the measured volume of the low irrigation was 64% of the mean of measured volume at mean irrigation, while mean of the simulated yield was 37%. For the High irrigation, mean of the measured volume for the shortgrasses was 113% of mean of the measured volume at mean irrigation and mean of the simulated yield for the shortgrasses was 110%. The mean of measured volume for the tallgrasses in the high irrigation was 110% of the mean irrigation, while mean of the simulated yield was 127%. For both short and tallgrasses, when simulated alone, mean of the low

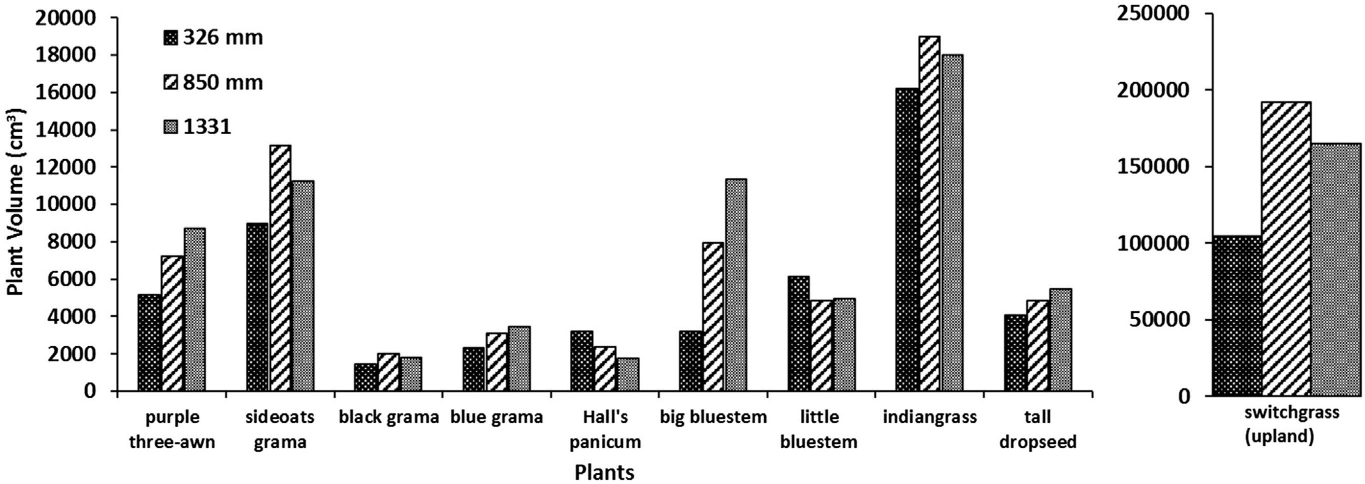

Fig. 2. Averaged plant volume estimation over 3 years under different rainfall treatment rates for 10 species used in this study.

Table 4
Leaf area index (LAI) and averaged biomass yield over 3 years under rainfall treatment rates simulated by ALMANAC.

Plants	LAI[a]	Simulated yield (t/ha)			LAI[a]	Simulated yield (t/ha)		
		Separately[b]				Competition[c]		
		350 mm	850 mm	1331 mm		350 mm	850 mm	1331 mm
Shortgrasses								
Purple three-awn	0.7	0.88	2.16	3	0.1	0.22	0.45	0.46
Black grama	1.5	0.79	1.98	2.12	0.3	0.09	0.14	0.15
Blue grama	1.5	0.89	2.19	2.46	0.3	0.11	0.21	0.23
Hall's panicum	1.5	0.9	2.18	2.4	0.3	0.19	0.59	0.6
Sideoats grama	2.5	0.84	2.11	2.21	0.4	0.32	0.84	0.84
Tallgrasses								
Big bluestem	3.3	1.46	4.03	5.2	0.6	0.57	1.23	1.54
Little bluestem	3	1.81	5.54	7.55	0.5	0.15	0.43	0.61
Indiangrass	3.1	1.21	3.54	4.55	0.5	0.11	0.33	0.44
Tall dropseed	2.7	1.69	5.30	7.15	0.5	0.04	0.11	0.12
Switchgrass (upland)	6.8	3.51	8.02	9.06	1.1	1.53	4.06	4.31

[a] Values of LAI were observed from database of ALMANAC (Kiniry et al., 1992).
[b] Simulating each species growing separately.
[c] Simulating all species growing together and competing.

measured treatment was 64% of the mean irrigation treatment while mean of the low simulated was 38% of the mean irrigation treatment. These values for high irrigation as compared to mean irrigation were 111% for measured and 119% for simulated.

When we simulated all species growing together and thus competing, the model results generally had a better fit to the measured data (Table 5). For the shortgrasses, the low irrigation treatment values were 64% and 51% for the measured and simulated respectively. For the tall grasses, the mean values were 64% and 47% for the low irrigation treatment. For the shortgrasses, high irrigation treatment, values were 113% and 104% for the measured and simulated, respectively. For the tallgrasses, the high irrigation values were 110% and 121% for the measured and simulated, respectively. For both short and tallgrasses in the low irrigation treatment, values were 64% and 49% for the measured and simulated values respectively. For the high irrigation treatment, these values were 111% and 113%.

Previous simulations of grass monocultures and native grass mixtures with ALMANAC consisted of successful comparisons of long-term runs with expected range site productivity for the special grass species or comparisons of simulations with actual years of weather to measured plot yields. Kiniry et al. (2002) simulated native grass mixtures in diverse sites in Texas and compared the simulations with published Natural Resource Conservation Service (NRCS) ecological site mean yields. Kiniry et al. (2013) simulated monoculture introduced grass species and native grass mixtures in diverse sites in Texas and compared the simulations with published NRCS ecological site mean yields. Kiniry et al. (2014) simulated western rangeland grass mixtures in Utah and New Mexico and compared them to published NRCS ecological site mean yields. Finally, managed switchgrass stands were simulated and compared with measured plot yields in sites at a wide range of latitudes in the U.S. (Kiniry et al., 2008a, 2008b).

These previous tests of ALMANAC with grass mixtures only compared the total mixture grass yield with the total simulated by ALMANAC. This study is the first in which actual measured yields of the individual grasses in the mixture were compared with the simulated yields of each grass. Successes and shortcomings reported herein are important as we attempt to apply such process-based models on range sites for conservation. Not all species are equally drought resistant (Julander, 1945), and understanding species variation can inform management and selection of range species in a drier future. Furthermore, grazing obviously is not uniform across grass species, with the most palatable grazed first and most intensively. Thus, although we did not address grazing here, the ability to simulate each species in the mixture becomes

Table 5
Relative ratio of 350 mm/850 mm and 1331 mm/850 mm for each of measured plant volume and simulated yield and ratio between relative measured plant volume and relative simulated yield ratios. Averaged values within two groups including shortgrasses and tallgrasses. Shortgrasses were grown together and had potential LAI values in the monoculture runs of 0.7–2.5 and 0.1–0.4 for the competition runs. Tall grasses were grown together and the potential LAI values in the monoculture runs were 2.5–6.8 and 0.5–1.1 for the competition runs.

Plants	350 mm/850 mm			1331 mm/850 mm		
	Mean Volume	Simulated yield Separate[a]	Simulated yield Competition[b]	Mean Volume	Simulated yield Separate[a]	Simulated yield Competition[b]
Shortgrasses						
Purple three-awn	0.71	0.41	0.48	1.2	1.02	1.03
Black grama	0.62	0.4	0.64	1.33	1.07	1.07
Blue grama	0.55	0.4	0.53	1.11	1.13	1.07
Hall's panicum	1.36	0.41	0.33	0.74	1.1	1.01
Sideoats grama	0.68	0.4	0.38	0.85	1.17	1.01
Average[c]	**0.64**	**0.40**	**0.51**	**1.13**	**1.10**	**1.04**
Tallgrasses						
Big bluestem	0.4	0.36	0.45	1.43	1.29	1.33
Little bluestem	1.27	0.32	0.43	1.02	1.37	1.54
Indiangrass	0.85	0.34	0.35	0.95	1.28	1.49
Tall dropseed	0.74	0.32	0.59	1.14	1.36	0.95
Switchgrass (Upland)	0.54	0.44	0.48	0.86	1.16	1.07
Average[d]	**0.64**	**0.37**	**0.47**	**1.10**	**1.27**	**1.21**
Both groups' Average[e]	**0.64**	**0.38**	**0.49**	**1.11**	**1.19**	**1.13**

[a] Simulating each species growing separately.
[b] Simulating all species growing together and competing.
[c] Averages calculated without Hall's panicum because of the outlier values for Mean Volume fractions.
[d] Averages calculated without little bluestem because of the outlier values for Mean Volume fractions.
[e] Averages calculated without little bluestem and Hall's panicum because of the outlier values for Mean Volume fraction.

vitally important when simulating grazing systems particularly given annual and regional variation in rainfall conditions. By using species-level data, we demonstrated that ALMANAC is accurate to within 23% on average as long as competition is included, but improvements are needed to better address some species and rainfall combinations that were off by over 100%.

It should be pointed out that there were anomalous results in the responses to irrigation, both in the measured volumes and in the simulated results. Both Hall's panicum and little bluestem showed greater mean values for measured volumes in the low irrigation treatment than in the mean irrigation treatment (Table 5). For the high irrigation treatment, measured values were lower than the mean irrigation treatment for Hall's panicum, sideoats grama, and indiangrass. The simulations with each species growing separately (Table 5), showed expected responses, with the lower irrigation always showing lower simulated yields relative to the mean and the high irrigation treatment always showing higher simulated values than the mean irrigation treatment. Thus care should be taken when interpreting these results for individual species. While the means by groups followed expected trends with irrigations, variation among species in measurements had some unexpected values.

4. Conclusion

In conclusion, results from this study indicate that there is variation in plant growth responses among ten forage grasses to either various rainfall rates, soil types, or both. In general, most of species significantly increased basal diameter and height as rainfall increased. Soil texture also significantly effect on plant height for some of Great Plains prairie grasses. In both measured volume and simulated yield, large increases were observed between 350 mm/yr and 850 mm/yr for all species, while a relative small increases were observed at 1331 mm/yr. Simulated yields when simulating either each species separately or all species growing together relatively agree well with measurement in comparison between medium and high rainfall treatment. But, in comparison between low and medium rainfall treatments, simulated yields with all species growing together gave better agreement with measurements.

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