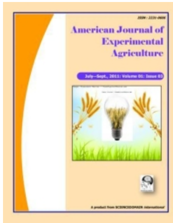

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Novel Application of ALMANAC: Modelling a Functional Group, Exotic Warm-season Perennial Grasses

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Authors' contributions

This work was carried out in collaboration between all authors. Authors JRK, MVVJ, BCV and BLB designed the study, performed the statistical analysis, wrote the protocol, and wrote the first draft of the manuscript. Authors JRK and MVVJ managed the analyses of the study. All four authors managed the literature searches. Authors JRK, MVVJ and BLB read and approved the final manuscript.

Research Article

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ABSTRACT

Aim: To determine the efficacy of the ALMANAC model in simulating leaf canopy growth and biomass production of a plant functional group, specifically "exotic warm-season perennial grasses," represented by buffelgrass [*Pennisetum ciliare* (L.) Link] and "Old World Bluestems" (*Bothriochloa* Kuntze, *Capillipedium* Stapf, and *Dichanthium* Willemet).
Study Design: Leaf area index (LAI) over the growing season, the light extinction coefficient (*k*) for Beer's Law, and the radiation use efficiency (RUE) were quantified for Old World Bluestems and buffelgrass.
Place and Duration of Study: This study was conducted in central Oklahoma in 2005 and

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2007 and in south-central Texas in 2008 and 2009.
Methodology: Serial dates of measurement over the growing season of leaf area index, light extinction coefficient for Beer's Law, and the radiation use efficiency were used to quantify these growth parameters for simulation modeling.
Results: All assayed grasses in the exotic warm-season perennial grasses functional group had similar values for LAI (mean = 4), *k* (mean = -0.5), and RUE (mean = 1.3 g MJ^{-1} IPAR).
Conclusion: When these parameters were applied in a simulation model, the model successfully simulated mean yields near the reported yields for exotic warm-season perennial grasses on all simulated soils in Texas and Oklahoma and in Mexico. These results suggest that with further parameterization, the applicability of such process-based models could be expanded from species simulation to functional group simulation, whereby land managers could determine potential adaptability, water use, soil erosion, and forage productivity of various plant functional groups over a wide range of soils and climatic conditions.

Keywords: ALMANAC: Agricultural Land Management Alternatives with Numerical Assessment Criteria; APEX: Agricultural Policy/Environmental eXtender; FIPAR: Fraction of Photosynthetically Active Radiation Intercepted by the Plant Canopy; IPAR: Intercepted Photosynthetically Active Radiation; LAI: Leaf Area Index; OWB: Old World Bluestems; RUE: Radiation Use Efficiency; PAR: Photosynthetically Active Radiation.

1. INTRODUCTION

Easily established exotic warm-season perennial grasses have been and continue to be intentionally introduced outside of their native ranges. Such introductions are often both beneficial and deleterious: soil stabilization and carrying capacity may increase, while biodiversity is reduced and nutrient and water cycles are changed. In the United States, two representative exotic warm-season perennial grasses are buffelgrass [*Pennisetum ciliare* (L.) Link] and old world bluestem (OWB) (genera *Bothriochloa* Kuntze, *Capillipedium* Stapf, and *Dichanthium* Willemet) [1]. In the prairies of the U.S. the greatest threats to native systems may be from species belonging to the same ecosystem-level functional group as the dominant species, the warm-season perennial grasses [2,3]. However, even with potential for deleterious ecological effects, exotic warm-season perennial grasses, including buffelgrass and OWB, are valued by ranchers and land managers. It is imperative to identify management strategies for the users of these grasses such that production benefits are maximized and environmental impacts are realistically simulated and assessed over relevant regions [4].

Exotic perennial grasses tend to be superior competitors for limiting resources, which allows them to establish easily [5], spread aggressively and dominate areas in which they were not originally planted [6]. Buffelgrass is adapted to a wide range of soils, is exceptionally drought tolerant, able to respond quickly to available moisture, and is extremely tolerant to grazing [7], characteristics which have made buffelgrass an effective grass for stabilizing soils and increasing carrying capacity [6]. Buffelgrass also tends to produce more biomass than native grasses adapted to semi-arid areas [6]. However, buffelgrass is not suitable to all sites. In Sonora Mexico, ranchers hoping to increase productivity actually lowered carrying capacity by replacing native vegetation with buffelgrass [8].

Old World Bluestems (OWB) tend to outcompete native species in their functional group, due to their production potential, tolerance to grazing and drought, and ability to respond efficiently and quickly to limited available resources [2,9,10]. Old World Bluestems are effective at establishing in areas where they were not previously planted, particularly when areas are disturbed [11]. To the benefit of livestock producers, OWB can produce up to six times more biomass than locally adapted native species. Such gains in biomass can be detrimental to local biodiversity [12] and native biomass production [3].

The ability of OWB and buffelgrass to dominate landscapes has led to a number of deleterious consequences. Buffelgrass and OWB establishment and spread is linked to declines in species richness and diversity [7,10,13-17]. Additionally, exotic grasses which produce more biomass than native species can, if not properly grazed, promote hotter and more frequent fires, which may have profound impacts on ecosystem structure and function, including water and nutrient cycling, as well as carrying capacity [2,18].

The implications of studies on OWB and buffelgrass tend to be limited in scope, as research is typically limited to one species and one geographical context [17]. Considering plants in the context of functional groups rather than as species allows one to expand the implications beyond a single-species study. Old World Bluestems and buffelgrass typify the exotic warm-season perennial grass functional group and are widely established in the central, southern, and southwestern U.S. Both are considered strong competitors with native warm-season perennial grasses. Shared features allow these grasses to be simulated as a generalized functional group rather than as individual species.

With robust process-based simulation models, conclusions of past studies can be applied to new areas to determine potential adaptation and spread of these grasses into areas not currently assayed. Such models, based on key processes, can be valuable tools to evaluate environmental consequences such as soil erosion, changes in soil carbon, and changes in grazing potential, of these type grasses as compared to native plant communities on different range sites. Process-based models that realistically simulate leaf canopy area growth and biomass production of grasses in the functional group represented by buffelgrass and OWB would be valuable to land managers interested in how well these grasses could establish and spread on their lands, regardless of whether their interest is driven by a desire to increase productivity of livestock forage or a desire to maintain biodiversity. Such models would be valuable to anyone interested in the impacts of management of these grasses on hydrology, soil erosion, nutrient cycling, and wildlife habitat in regions of interest.

Physiologically-based growth characteristics contributing to high competitive ability have not been generally identified, let alone quantified. The scientific literature asserts a multitude of mechanisms by which invasive species displace native species: greater phenotypic plasticity, higher fecundity rates, higher leaf area, and lower quality tissues [19]; allelopathy [20]; absence of natural enemies [21]; higher water use efficiency [22], higher radiation use efficiency [23]; evolutionary genetics [24]; increased competitive ability [25]; contemporary evolution [26]; and ability to capitalize on vulnerabilities due to low biodiversity [26].

The basic premise of this project was that growth parameters developed in well managed stands of representative species within a functional group would describe potential growth of other species within the same functional group. Further, we hypothesized that plant growth simulation models such as ALMANAC (Agricultural Land Management Alternatives with Numerical Assessment Criteria) [27] and APEX (Agricultural Policy/Environmental eXtender) [28] could simulate not just single species, but functional groups across broad geographical distributions. Once calibrated, these models, with their daily time step and nutrient and water balances, could be applied to any species in this functional group in field situations where nutrient limitation, drought, herbivory, and competition with other species occur. Advantages of these models over commonly used empirical models include that they are mechanistic, process-based, and easily transferred among sites. This approach has demonstrated reasonable results for a multitude of species on diverse soil types under a variable range of precipitation across the U.S. [29-30].

The first objective of this project was to calibrate the ALMANAC model for the exotic perennial warm season grass functional group. This required quantification of the leaf area index (LAI) during the growing season, the light extinction coefficient (*k*) in Beer's Law, and the radiation use efficiency (RUE) for species within this functional group. Two species were selected which occur across a broad geographical range to assay for these physiological parameters: OWB and buffelgrass. Data were collected for OWB in central Oklahoma and for buffelgrass in south-central Texas. Second, the accuracy of these quantified parameters was tested by inputting them into the ALMANAC model and simulating exotic perennial warm season grass biomass production on high and low yielding soils in southern Texas and Oklahoma. ALMANAC output was compared to USDA-NRCS reported dry weight yields for the same functional group in the same areas. Finally, the broad applicability of the parameters was tested by simulating exotic perennial warm season grass performance on two sites previously described in published studies, one in Starr County, TX [31] and one in Sonora, Mexico [32].

2. MATERIALS AND METHODS

Parameters were derived for OWB on a Pond Creek fine-silty loam soil (mixed, superactive, thermic Pachic Argiustolls) at the USDA-ARS Grazinglands Research Laboratory near El Reno, OK (35°32'N, 97°57'W, 432 m a.s.l). Plots were in an established plant stand, with an exclusion fence to prevent livestock grazing. Plant measurements were taken at two week intervals during the growing season in 2005 and 2007.

Four buffelgrass cultivars were established at the Texas A&M University Farm near College Station, Texas (30°32'N, 96°25'W, 73 m a.s.l.). Plots of 'Frio' were established from seedlings in 2003 and plots of 'Common', 'Nueces', and 'Llano' were established from seedlings in 2007. The Frio plots were on Belk clay (fine, mixed, active thermic Entic Hapaluderts) and the Common, Nueces, and Llano plots were on Weswood silt loam (fine-silty, mixed superactive, thermic Udifluventic Haplustepts). There was 1 m between plants and 1 m row spacing. Plant measurements were taken at two week intervals during the growing season in 2008 and 2009.

Data collection consisted of photosynthetically active radiation (PAR) intercepted by the green plant canopy followed by destructive harvests of a given ground area of green plant canopy. Samples were put in coolers to avoid desiccation, transported to a laboratory, and weighed fresh. A subsample was then weighed fresh and the leaf area of the subsample was measured with a Licor LI-3100C area meter (Li-Cor Biosciences, Lincoln, NE). Leaf area of the entire sample was calculated from the subsample leaf area multiplied by the ratio of total fresh weight divided by subsample fresh weight. LAI (unitless) was calculated as the total leaf area divided by the sampled ground area. The entire sample was then dried in a forced air oven at 70° C until constant weight was achieved and the dry weight measured.
Light extinction coefficient (*k*) was determined from the LAI and the mean fraction of PAR intercepted by the plant canopy (FIPAR). At each sample point six PAR measurements were

taken simultaneously below and above the photosynthetic portions of the canopy. Measurements of PAR were taken below the plant canopy using a Decagon Accupar LP-80 ceptometer (Decagon, Inc., Pullman, WA), while an external sensor measured PAR above the vegetation to be harvested. FIPAR was calculated as the mean of 1-PAR_{below}/PAR_{above}.

Values for RUE (g of dry weight per MJ intercepted PAR) were calculated from the regression of cumulative dry weight biomass (per m^2 ground area) divided by summed intercepted IPAR (MJ per m^2 ground area). Daily values for FIPAR were calculated by linearly interpolating FIPAR between sampling dates. Daily values for summed IPAR (intercepted photosynthetically active radiation) were calculated from the daily value for FIPAR and the incident PAR (45% of total solar radiation, [33]). Numbers of data points varied among the locations, years, and grasses due to different sampling frequencies and different intervals of active growth.

2.1 ALMANAC Model

The ALMANAC model is a relevant model for species specific perennial grass simulation, in terms of biomass production, and impacts on nutrient and water cycling [29,30,34,35]. ALMANAC relies on inputs of readily available daily weather data and the extensive USDA-NRCS soils data. Commonly reported values of daily maximum and minimum temperatures, rainfall, and solar radiation are also inputs. This enables users to easily apply the model to their particular area by using readily available soils data and climate data from the nearest weather station. The model uses a daily time step, making it capable of rapidly simulating multiple years of plant growth in a few seconds. ALMANAC efficiently simulates an extensive range plant species under diverse soil and weather scenarios, as well as under a variety of land management options, including tillage, various harvest heights, nutrient management, and grazing.

The ALMANAC model simulates the interactions between soil water balance and plant growth processes, including light interception by photosynthetic tissues, dry weight production, and partitioning of biomass into reproductive and vegetative structures. ALMANAC simulates LAI, light interception with Beer's law, and potential daily biomass increase with a species- or functional group-specific value of RUE. The model uses the canopy level RUE approach to simulate biomass growth instead of the more complex approach with CO_2 accumulation via photosynthesis. This precludes the need for detailed calculation of carbon partitioning, leaf level carbon exchange rates, and respiration. In addition, the canopy level model is less demanding for inputs. The maximum LAI of a species at high planting density is an input parameter. When available water in the current rooting depth of the species of interest, light, or nutrients are insufficient to meet potential evapotranspiration, photosynthetic needs, and nutrient needs ALMANAC simulates a reduction in LAI and biomass accumulation. The potential LAI is also reduced as a function of planting density. Plant development is temperature driven, with duration of growth stages dependent on degree days. To date, each plant species has a defined base temperature and optimum temperature. In this analysis, the functional group being simulated, which encompasses a number of species, also has a unique defined base temperature and optimum temperature.

Critical for plant biomass simulation in water-limited conditions is the simulated water demand. Potential evaporation (*E*o) is calculated first, and then potential soil water evaporation (*E*s) and potential plant water transpiration (*E*p) are derived from *E*o and leaf area index (LAI). Based on the soil water supply and plant water demand, a water stress factor is estimated to decrease daily plant growth, E_S and E_P were estimated by

$$E_P = Eo(LAI/3)\ for\ 0 < LAI < 3.0 \quad [1]$$

$$E_P = Eo\ for\ LAI > 3.0 \quad [2]$$

E_S is either *E*o exp(-0.1BIO) or *E*o-*E*p, whichever is smallest, where BIO is the sum of aboveground biomass and plant residue (Mg ha^{-1}). Water stress factor is the ratio of water use to water demand (*E*p), and water use is a function of plant extractable water and root depth. If available water in the current rooting zone is sufficient to meet demand, then water use equals *E*p. Otherwise, water use is restricted to the water available in the current rooting zone.

2.2 Simulations of Exotic Perennial Warm Season Grasses as Compared to NRCS Ecological Site Productivity Reported for Representative Species

Areas simulated in this part of the study include two soils in each of two counties in Oklahoma and two soils in each of two counties in southern Texas. The counties simulated were selected because they had soils with quantified annual biomass yields for a representative grass in the functional group (OWB in OK and buffelgrass in TX) reported for both a dominant high-yielding and a dominant low-yielding soil (NRCS Web Soil Survey) (http://websoilsurvey.nrcs.usda.gov/app/HomePage.htm). NRCS reported total annual production values were derived from at least 3 years of end of season sampling on sites with closed canopy stands of the species of interest. The standardized NRCS procedure measured dry matter biomass production above a 5 cm cutting height in at least 10 randomly selected sample plots at each reference field site.

In Woodward County (county seat Woodward, OK, 36º26′N, 99º24′ W, elev. 582 m) we simulated exotic warm-season perennial grass biomass production on a loamy prairie site (Westview soil:fine-silty, mixed, superactive, thermic Pachic Argiustolls) and a sandy loam prairie site (Hardeman soil: coarse-loamy, mixed, superactive, thermic Typic Haplustepts). In Payne County (county seat Stillwater, OK) (36º8′N, 97º 11′W, elev. 292 m), we simulated a loamy prairie site (Bethany soil:fine, mixed, superactive, thermic Pachic Paleustolls) and a loamy bottomland site (Pulasky soil: coarse-loamy, mixed, superactive, nonacid, thermic Udic Ustifluvents). In Webb County (county seat Laredo, TX) (27°32'N, 99°29'W, elev. 155 m), we simulated exotic warm season perennial grass biomass production on a gray sandy loam site (Copita soil:fine-loamy, mixed, superactive, hyperthermic Aridic Calciustepts) and a saline clay loam site (Moglia soil: fine-loamy, mixed, superactive, hyperthermic Aridic Calciustepts). In Kenedy County (county seat Sarita, TX) (26 º52′N, 97º44′W, elev. 11 m) we simulated a clay loam site (Czar soil: fine-loamy, mixed, superactive, hyperthermic Pachic Argiustolls) and a sandy site (Padrones soil: loamy, mixed, active, hyperthermic Arenic Natrustalfs).

Mean simulated yield over 10 years of real weather data were compared to the reported annual production (from USDA-NRCS Web Soil Survey) for each site. The NRCS value of Animal Unit Month (AUM) was converted to Mg ha^{-1} (0% moisture) with a conversion factor assuming 700 lbs (318 kg) of air dried biomass (90% moisture) per AUM. The representative exotic warm season perennial grass at the Oklahoma sites was OWB, listed in the Web Soil

Survey as “introduced bluestem”. In Texas the representative species for yield comparisons was buffelgrass.

Values for key plant parameters for the functional group were derived from the field measurement results described below. Values for potential LAI were assumed to be 3.6 in all cases except two. For the two lower yielding Oklahoma sites, it was assumed that a much lower plant stand occurred and potential LAI was assumed to be 0.1. Values for duration of the growing season were assumed to be 800 degree days base 12ºC. This base temperature was based on results with switchgrass (*Panicum virgatum* L.) as described by Kiniry et al. [29]. Switchgrass is a warm season perennial grass native to North America. The radiation use efficiency was assumed to be 1.85 g per MJ intercepted PAR and the light extinction coefficient (*k*) was assumed to be -0.5 for the exotic perennial warm season grass functional group. The RUE value was derived from the multi-year mean for Common buffelgrass (1.38) and the first year value for OWB (1.24), with the assumption that 31% of total biomass is partitioned to the roots. Similar partitioning (30 to 37%) was measured for sideoats grama [*Bouteloua curtipendula* (Michaux) Torrey] and switchgrass during a wet year at Temple, TX [31].

2.3 Buffelgrass Simulations at Two Sites

In South Texas, Gonzales and Dodd [32] reported buffelgrass dry weight yields for four years at a 430 mm mean annual precipitation site following mechanical brush manipulation. The study area (“on the southern edge of the Rio Grande Plain about 38 km north of Rio Grande City, Starr County, Texas”, exact location not specified) was a sandy loam range site with Brennan soils (fine-loamy, mixed, hyperthermic Aridic Hasplustalfs) and McAllen soils (fine sandy loam hyperthermic Aridic Ustochrepts). The mean measured production data from two brush manipulation treatments (root plowing and front-end stacking) was used for comparison with simulations.

In Mexico, Martin-R et al. [33] reported buffelgrass dry weight yields for three years at a 320 mm mean annual precipitation site. The study area was on an Anthony fine loam (thermic Typic Torrifluvents). The site was 82 km north of Hermosillo (29º41′N, 115º57′W). Actual weather data for this site was not available, so mean monthly values were used for Hermosillo. Monthly rainfall was adjusted to match those reported for the study site, and 15 years of simulated weather generated by the ALMANAC model was used. The simulated yield for the 15 years were ranked and the mean of the lowest 5 years compared to the lowest yielding measured mean, the mean of the middle 5 simulated yields compared to the mean of the intermediate measured yield, and the mean of the highest 5 simulated yields compared to the highest measured yield.

3. RESULTS

The values for the OWB and the four buffelgrass cultivars were similar in their values for LAI, light extinction coefficient (*k*), and RUE. For both species, the mean maximum LAI values for the season were near 4 and the mean *k* values were near -0.5. The mean RUE for both species, with all buffelgrass cultivars combined, was 1.3 g MJ^{-1} IPAR.

Weather conditions during the growing seasons at El Reno, OK were typical of this region, with mean monthly temperatures near 29 to 32ºC during June and July, high values for incident solar radiation, and precipitation adequate to sustain grass growth (Table 1). Solar radiation means were similar to long term monthly means. Rainfall sums for the five months were below average in 2005 and above average in 2007. During 2005, rainfall from March through June was below average, but with more than 75 mm each month after April, which provided sufficient moisture to preclude drought stress. In 2007, there was above-average rainfall during every month of the growing season except for April, which was near the average. Likewise, monthly temperature values were near the averages for all the months after March.

The LAI values for OWB at El Reno showed much different patterns and maximums between the two years (Table 2). The mean overall LAI for both years combined was 3.57. During the first year, the LAI peaked on 14 June and the second year it peaked on 18 July. The earlier date for attaining the maximum in the first year resulted in a shorter growing season and a much lower maximum LAI of 2.79, as compared to 4.35 in the second year. During the first year, the LAI decreased dramatically by 28 July, much different than in the second year.

The light extinction coefficient (*k*) values for Beer's Law were generally greater in the second year, but there was much variability among sampling dates. Values became very large after maximum LAI was attained, presumably due to extra light interception by the senescent leaves, and they were not accounted for in the calculation of k for each date. Thus we only considered values up to the date of maximum LAI each year, for the calculation of mean *k*. This consisted of two dates for 2005 (mean *k* was -0.37) and four dates for 2007 (mean *k* was -0.55). Overall mean *k* for both years was -0.46.

The RUE values within each year had regressions with high correlation coefficients (r^2 greater than 0.9 in each case) and the RUE values were between 1.1 and 1.3 (Fig. 1). Regressions were significant in every case (Table 3). The mean RUE over both years was 1.18 g MJ^{-1}.

Weather conditions during the two growing seasons at College Station, TX were much drier than normal, especially after April 2008 and during the entire 2009 growing season (Table 1). Plants relied on stored soil moisture from winter rainfall and preseason supplemental irrigation to sustain growth. Solar radiation means were somewhat lower than long term monthly means, possibly due to greater cloud cover during the growing season than normal. Average maximum monthly temperatures were 1 to 3 degrees greater than the long term means for June and July of both years.

Buffelgrass LAI values varied both between years and among the four cultivars measured (Table 4). The mean LAI for both years combined was greatest for Common and Nueces and least for Frio. The maximum LAI values were greater for the first year for Common and Nueces and greater in the second year for Frio and Llano. There was not a consistent trend between years as to which cultivar reached its maximum LAI earliest. In 2008, Common and Llano reached their maximums first, while in 2009 Nueces reached its maximum first.

Table 1. Mean monthly growing season weather averages, and precipitation totals measured at the field plots at El Reno, OK and College Station, TX

Yr	Month	Location	Max temp	Min temp	Solar radiation	Precipitation
			°C	°C	$MJ\ m^{-2}\ d^{-1}$	mm
2005	March	El Reno, OK	16.7	3.3	16	14
	April		21.7	7.2	22	7
	May		25.6	13.9	19	84
	June		31.6	18.1	25	88
	July		32.6	18.7	26	75
	Sum					268
2007	March		20.6	7.2	14	134
	April		18.9	6.1	17	75
	May		25.3	14.7	18	280
	June		28.6	17.9	18	316
	July		31.3	19.1	22	88
	Sum					893
Long-term means	March		16.7	1.7	17	56
	April		21.7	7.2	21	76
	May		26.7	14.4	22	148
	June		31.1	18.3	26	125
	July		34.4	21.1	26	67
	Sum					472
2008	March	College Station, TX[1]	22.9	9.5	16	70
	April		26.6	14.0	17	71
	May		30.1	18.5	19	18
	June		35.9	22.6	15	7
	July		26.2	21.6	24	5
	Sum					171
2009	March		22.8	9.5	12	2
	April		25.4	13.0	17	3
	May		30.9	19.0	15	0
	June		36.9	22.4	13	0
	July		38.0	24.1	22	9
	Sum					14
Long-term means	March		22.8	10.0	18	72
	April		26.1	13.9	19	81
	May		29.4	18.3	23	128
	June		33.3	22.2	25	96
	July		35.6	21.7	26	49
	Sum					426

[1]Plots at College Station Texas were flood-irrigated prior to initiation of the growing season, to refill the soil profile each year.

Table 2. Old World Bluestem mean LAI and k values measured at El Reno, OK. Mean k for the two years was -0.46 and overall mean maximum LAI was 3.57. Bold LAI values were the maximums in each season

Date	Mean LAI	Mean k
06/02/05	1.91	-0.29
06/14/05	2.79	-0.45
06/29/05	2.54	-1.04
07/13/05	2.72	-1.29
07/28/05	1.25	-2.35
Mean[1]		-0.37
05/16/07	1.01	-0.50
05/31/07	2.16	-0.37
06/13/07	3.38	-0.61
07/18/07	4.35	-0.71
08/01/07	3.48	-1.51
Mean[1]		-0.55

[1]Mean k calculated for dates prior to decreasing LAI (thus before senescent leaves are increasing the absolute value of k). These consist of the first two measurement dates in 2005 and the first four dates in 2007.

Table 3. Values for adjusted coefficients of determination (R_α^2), F ratios (F), and *p values* for each regression of Figures 1 to 5

	Year	R_α^2	F	*p values*
Old World Bluestem in El Reno, OK	2005	0.94	59.4	<0.005
	2007	0.91	201.9	<0.001
Frio Buffelgrass in College Stn., TX	2008	0.48	13.8	<0.005
	2009	0.77	57.6	<0.001
Common Buffelgrass in College Stn., TX	2008	0.65	21.6	<0.001
	2009	0.58	24.1	<0.001
Llano Buffelgrass in College Stn., TX	2008	0.79	55.0	<0.001
	2009	0.75	51.9	<0.001
Neuces Buffelgrass in College Stn., TX	2008	0.88	104.7	<0.001
	2009	0.56	22.2	<0.001

Table 4. Buffelgrass means for LAI and k values measured near College Station, TX. Mean k for the four ecotypes was -0.48 in 2008 and -0.55 in 2009 for an overall mean k of -0.52. Overall mean maximum LAI was 4.04. Bold LAI values were the maximums in each in each season

Ecotype	Frio		Common		Llano		Nueces	
Date	**LAI**	**k**	**LAI**	**k**	**LAI**	**k**	**LAI**	**k**
04/30/08	0.89	-0.47	1.46	-0.44	1.30	-0.45		
05/13/08	0.85	-0.62	2.13	-0.52	2.32	-0.47	1.72	-0.52
05/28/08	1.75	-0.57	3.06	-0.36	2.76	-0.47	2.40	-0.50
06/10/08	1.88	-0.47	**5.90**	-0.40	**3.14**	-0.52	**4.40**	-0.41
06/24/08	**2.28**	-0.56	—[2]	—[2]	2.74	-0.74	3.93	-0.68
07/07/08	1.30	-0.67	—[2]	—[2]	2.46	-0.75	4.87	-0.45
Means[1]		-0.54		-0.43		-0.48		-0.48
05/13/09	0.76	-0.77	2.73	-0.44	2.17	-0.62	2.48	-0.54
05/27/09	1.56	-0.45	2.41	-0.62	2.19	-0.63	**4.33**	-0.41
06/24/09	1.75	-0.62	2.12	-0.71	1.88	-0.54	1.81	-0.60
07/07/09	**3.97**	-0.43	**3.42**	-0.57	**4.69**	-0.49	4.04	-0.44
Mean k values[1]		-0.57		-0.58		-0.57		-0.48
Mean max LAI values	3.12		4.66		3.92		4.45	

[1]Mean k calculated for dates prior to decreasing LAI in 2008 (thus before senescent leaves are increasing the absolute value of k). In 2008 these consist of the first five measurement dates for Frio, all four dates for Common, the first four dates for Llano, and the first three dates for Nueces. Used all dates in 2009 for the first three ecotypes since LAI was greatest on the last date. Used only the first two dates for Nueces in 2009 since the LAI was greatest on the second date.
[2]—, data not collected.

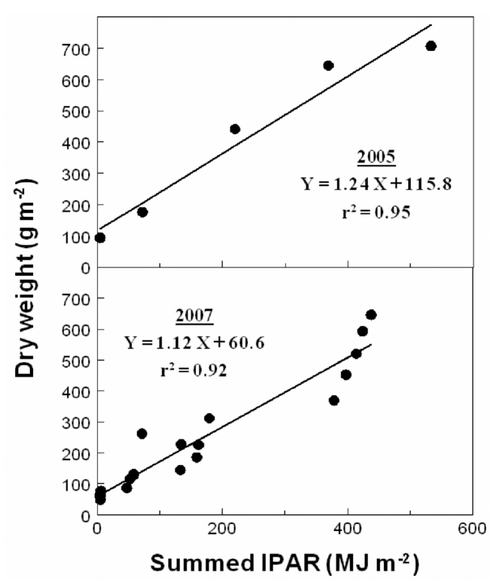

Fig. 1. Old World Bluestem at El Reno, OK: RUE calculation for two years. Regression calculated with the data values for the first four dates in each year

The light extinction coefficient (*k*) values for Beer's Law were similar between years, with an overall mean k for all cultivars over both years being -0.52. Similar to the buffelgrass results above, in the few cases with decreasing LAI after the maximum was measured, values usually became greater. Again, only values up to the date of maximum LAI were considered each year for the calculation of mean k for each cultivar. There was not a consistent pattern between years as to one cultivar having a greater or smaller k value than the other cultivars.

The RUE values within each year had regressions with lower correlation coefficients than OWB (r^2 values of 0.52 to 0.89) and the RUE values were between 1.0 and 2.0, with two exceptions (Figs. 2-5). The mean RUE over both years was 1.32 g MJ^{-1}. Cultivars failed to show consistent rankings between years, with Common and Nueces having the greatest RUE values in 2008 and Llano and Nueces having the greatest values in 2009. One observation was that the mean RUE values over both years showed Llano and Common having similar means (1.42 and 1.38 g MJ^{-1}, respectively), Nueces having the greatest mean (1.51 g MJ^{-1}), and Frio having the lowest mean (0.98 g MJ^{-1}).

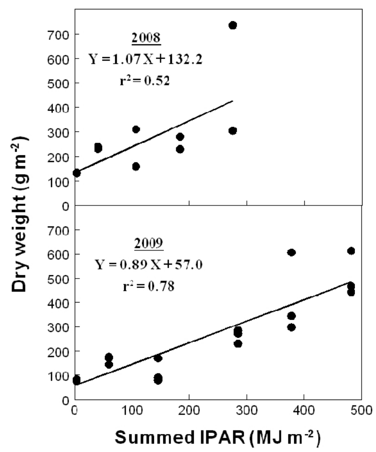

Fig. 2. Frio buffelgrass at College Station, TX: RUE calculation for two years. Regression calculated with the data values for all measurement dates

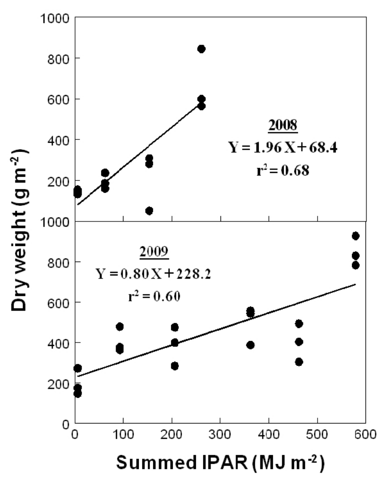

Fig. 3. Common buffelgrass at College Station, TX: RUE calculation for two years. Regression calculated with the data values for all measurement dates

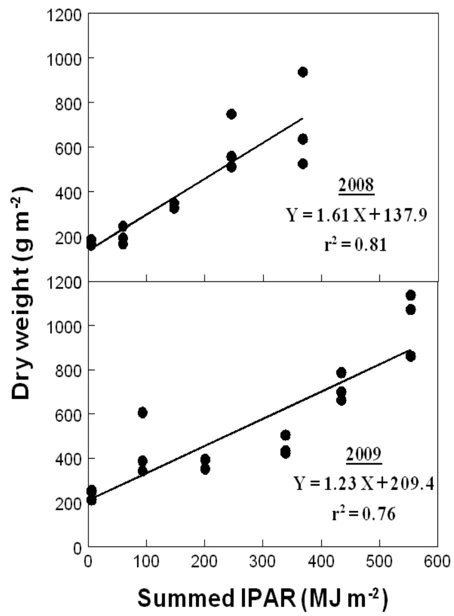

Fig. 4. Llano buffelgrass at College Station, TX: RUE calculation for two years. Regression calculated with the data values for all measurement dates

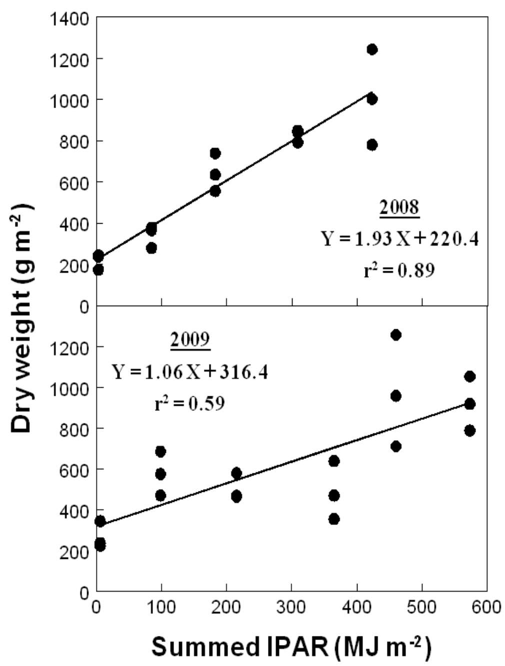

Fig. 5. Nueces buffelgrass at College Station, TX: RUE calculation for two years. Regression calculated with the data values for all measurement dates

3.1 Simulations of OWB (in OK) and Buffelgrass (in southern TX) as Compared to NRCS Ecological Site Productivity

For the Woodward County, OK simulated site, mean temperatures were similar to those experienced during the plant measurements at El Reno for the first four months of the growing season, but were 2 to 4ºC warmer for July (Tables 1 and 5). For Payne County, monthly maximums were less than 1ºC warmer than for El Reno for April, May and July.

For rainfall, the Woodward County site mean sum for the five months was below the average normally experienced at El Reno, nearer the value experienced in the drier, 2005 season at El Reno. For Payne County, rainfall was higher than normally experienced at El Reno, closer to what was experienced in the wetter, 2007 season at El Reno.

For the two sites in southern Texas simulated for buffelgrass, temperatures were warmer for the simulated sites for March-May and similar thereafter. The first three months had averages 0.5 to 4 degrees greater than experienced in the two growing season in College Station.

For rainfall at the two southern Texas sites, sums for the five months were below what is normally experienced for College Station, but near the 2008 sum. The mean sum for Kenedy County was 244 mm and the mean sum for Webb County was 176 mm, while the sum for College Station in 2009 was 171 mm.

The overall mean simulated values for buffelgrass and OWB were reasonable, within 10% of reported means (Table 6). The mean simulated overall for buffelgrass was 103% of the mean NRCS reported value. The mean simulated overall for OWB was 92% of the mean NRCS reported value. The model showed lower yields for the lower yielding soils in each case, as expected. The simulations for buffelgrass on the high yielding soils were 82 and 89% of NRCS values. Correspondingly, the means for buffelgrass on the low yielding soils were 99 and 143 percent of the NRCS values. For OWB, the means on the two high yielding soils were 97 and 73 percent of the NRCS values. On the low yielding soils for OWB, the means were 100 and 96% of the NRCS values.

3.2 Simulations of Buffelgrass in Starr County, TX and in Sonora, Mexico as Compared to Published Productivity

In Starr County, TX the model did a realistic job of simulating mean yields over four years, but failed to track year-to-year variability (Table 7). Over all four years, the mean measured yield for the two brush treatments was 6.7 Mg ha^{-1}, while the mean simulated yield was 7.0 Mg ha^{-1}. Thus the simulated mean was only 5% greater than the measured mean. Excluding the first year (with the lowest measured yield) the mean measured was 7.5 Mg ha^{-1}, while the mean simulated yield for these three years was 7.1 Mg ha^{-1}, only 6% lower.

Neither the mean measured yields nor the simulated yields followed the trend in annual rainfall. The lowest rainfall year (1975), with only 344 mm, had the largest simulated yield and an intermediate measured yield. The highest rainfall year (1974) had the lowest simulated yield and an intermediate measured yield. Thus in both cases, the simulations and the measured production, yields were not controlled by low rainfall for buffelgrass in these four years at this site.

Simulations for Sonora, Mexico (Table 8) showed realistic overall agreement with measured values for the intermediate five years, but tended to underpredict yields in the lowest and highest yielding years. These results should be interpreted with caution. This is a comparison using simulated weather data and not actual weather data for the three measurement years. These results are more a demonstration of the potential application of a process based model to simulate aggressive grass production in this region than a direct validation.

Table 5. Mean monthly growing season weather averages, and precipitation totals simulated generated for ten years in Woodward and Payne counties, OK and Kenedy and Webb counties, TX

	Max temp	**Min temp**	**Solar radiation**	**Precipitation**
	°C	**°C**	**MJ m^{-2} d^{-1}**	**mm**
Woodward county, OK (mean annual precip.=567mm)				
March	15.0	0.4	17	44
April	22.7	6.5	21	54
May	27.4	12.4	23	103
June	31.9	17.4	26	72
July	36.2	20.6	26	61
Sum				334
Payne county, OK (mean annual precip.=899mm)				
March	14.0	1.4	17	44
April	22.3	7.8	22	66
May	27.1	14.0	23	148
June	31.0	18.7	26	108
July	34.9	21.9	27	45
Sum				811
Kenedy county, TX (mean annual precip.=528mm)				
March	25.8	11.0	17	13
April	30.4	15.7	18	29
May	32.2	19.5	22	90
June	34.4	21.6	25	62
July	36.2	22.7	26	50
Sum				244
Webb county, TX (mean annual precip.=530mm)				
March	26.7	13.2	17	9
April	31.2	17.1	18	34
May	33.7	20.9	22	65
June	35.5	22.6	25	49
July	37.3	23.9	26	19
Sum				176

Table 6. Annual productivity of buffelgrass in southern Texas and Old World Bluestems in Oklahoma. Values simulated by the ALMANAC model (Sim) with ten years of measured weather data and values (NRCS) reported by USDA-NRCS for the specified soils in these counties. The simulated values are means+SD. The ratio of mean simulated over NRCS reported values is S/M

	Buffelgrass in Texas						
Webb County				**Kenedy County**			
Soil				**Soil**			
Series	**NRCS**	**Sim.**	**S/M**	**Series**	**NRCS**	**Sim.**	**S/M**
	Mg ha^{-1} yr^{-1}				Mg ha^{-1} yr^{-1}		
Copita	5.25	4.29±1.26	0.82	Czar	4.37	3.90±1.29	0.89
Mogia	1.75	1.73±0.43	0.99	Padrones	2.62	3.75±1.15	1.43
	Old World Bluestems in Oklahoma						
	Woodward County			**Payne County**			
Soil				**Soil**			
Series	**NRCS**	**Sim.**	**S/M**	**Series**	**NRCS**	**Sim.**	**S/M**
	Mg ha^{-1} yr^{-1}				Mg ha^{-1} yr^{-1}		
Westview	3.50	3.40±1.23	0.97	Bethany	3.14	2.28±0.87	0.73
Hardeman	0.20	0.20±0.05	1.00	Pulasky	0.23	0.22±0.05	0.96

Table 7. Simulated (by the ALMANAC model) and measured (Gonzales and Dodd, 1979) annual productivity of buffelgrass in Starr County, Texas. Values were simulated by ALMANAC with measured weather data. The ratio of simulated yield over measured yield was 1.05 for all four years and was 0.94 for the last three years. Rootplow and Frontend are two techniques of brush management applied in the original study prior to planting buffelgrass

	Treatments' meas. Yields			**Annual**	
Year	**Rootplow**	**Frontend**	**Mean**	**Simulated**	**Rainfall**
	Mg ha^{-1} yr^{-1}				**Mm yr^{-1}**
1973	3.5	5.1	4.3	6.9	634
1974	6.8	7.4	7.1	6.7	878
1975	8.5	5.5	7.0	7.6	344
1976	9.3	7.6	8.5	6.8	794
Means			6.7	7.0	
Means of the last 3 years			7.5	7.1	

Table 8. Simulated (by the ALMANAC model) and measured [31] annual productivity of buffelgrass in Sonora, Mexico. Values were simulated by ALMANAC with 15 years of simulated weather data for Hermosillo, with rainfall corrected to reported values for the study site. Simulated yield values were for the lowest 5 years, the intermediate 5 years, and the largest five years. S/M is the ratio of simulated yield over measured yield

	Measured yields	**Simulated yields (Mean±SD)**	**S/M**
Mg ha^{-1} yr^{-1}			
Lowest	0.47	0.22±0.14	0.47
Intermediate	1.04	0.98±0.51	0.94
Largest	3.02	2.31±0.68	0.76
Means	1.51	1.17±1.01	0.77

4. DISCUSSION

Exotic grasses such as the ones in this study have a number of traits that enable them to displace native grasses and form monotypic stands. Land managers, invasive species biologists, ecologists, agronomists, and grass biologists are interested in understanding the mechanisms that enable some plant species to dominate and form monocultures while other species do not perform as well under the same conditions. High productivity and rapid leaf area expansion are just two of the candidate traits that may lead to dominance by such plant species. Other candidate traits which we did not explore include allelopathy, high water use efficiency, easy seedling establishment and early seedling establishment. The last two traits allow plants to monopolize water, light, and nutrients by rapid growth, causing more effective plant demand and displacing later germinating species.

In the case of OWB and buffelgrass, plant productivity, as indicated by the RUE values, did not show unusually high values relative to some of the common warm season native grasses previously studied. Actually, the RUE values of these grasses were in the low end of the range of RUE values previously described for some common native and exotic C_4 grasses. Thus, our results suggest that future research should explore mechanisms other than RUE variability between species or functional groups to explain their predominance in this geographical region. On the other hand, the observed maximal seasonal LAI values of near 4 could be considered high for the rainfall zones where these grasses dominate.

Finally, while uncertainties persist concerning the roles of RUE and LAI in OWB and buffelgrass prevalence, use of these derived parameters in the ALMANAC model successfully simulated the biomass of these two species in the different validation sites. The accuracy of biomass predictions demonstrated that the model could complement field studies and serve as a valuable tool in evaluating management of these grasses and their impact on forage productivity of a site, soil erosion, water use, nutrient cycling, and wildlife habitat. Future applications of more detailed CO_2 photosynthetic simulation models [37-40] in this context will be interesting, in light of the differences between simulated and measured values in this study.

5. CONCLUSION

When the parameters derived in this study were applied in a simulation model, the model successfully simulated mean yields near the reported yields for exotic warm-season perennial grasses on all simulated soils in Texas and Oklahoma and in Mexico. These results suggest that with further parameterization, the applicability of such process-based models could be expanded from species simulation to functional group simulation, whereby land managers could determine potential adaptability, water use, soil erosion, and forage productivity of various plant functional groups over a wide range of soils and climatic conditions.

COMPETING INTERESTS

The authors have declared that no competing interests exist.

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