Ecological Modelling 351 (2017) 24–35

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Process-based simulation of prairie growth

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ARTICLE INFO

Article history:
Received 27 September 2016
Received in revised form 9 January 2017
Accepted 6 February 2017

Keywords:
APEX
Root:shoot ratio
Biomass
Simulation
Water stress
Interspecific competition

ABSTRACT

When field research is cost- or time-prohibitive, models can inform decision-makers regarding the impact of agricultural policy on production and the environment, but process-based models that simulate animal-plant-soil interaction and ecosystem services in grazing lands are rare. In the U.S.A., APEX (Agricultural Policy/Environmental eXtender) is a model commonly used to inform policy on cropland, but its ability to simulate grazinglands was less robust. Therefore, we enhanced the APEX model's plant growth module to improve its utility on grazing lands. Improvements addressed allocation of new biomass, response to water stress, competition for soil water, and regrowth of herbaceous perennials. Sensitivity analysis demonstrated that simulated biomass responded to changes in precipitation through adjustments to both total biomass and distribution of biomass aboveground and belowground. A deep-rooted species generally outperformed a shallow-rooted species but the relative advantage was greatest when precipitation was historically low. A 10-year dataset of peak biomass collected in central Kansas, U.S.A., was divided among 5 species and species groups and was used for calibration and validation. When the mass of all species was combined in the validation dataset, the percent bias was −2%, Willmott's D_r was 0.79, and r^2 was 0.84. When biomass production of individual species was analyzed, the model did not perform as well, with the percent bias ranging from −36 to 29%, Willmott's D_r ranging from 0.58 to 0.71, and r^2 from 0.25 to 0.67. Because grazing lands often have a rich species diversity, the improvements made APEX better-suited to modeling such heterogeneous landscapes. However, simulating biomass of individual species, rather than the sum of all species, is an area that still needs improvement. Further testing at additional sites to calibrate single- and multiple-species growth and identify any spatial trends in model performance will also be beneficial.

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1. Introduction

Grazinglands cover approximately 40% of the global terrestrial landmass (FAO, 2005) and store approximately 10% of its soil carbon (Nosberger et al., 2000). Conservative management of grazinglands can maintain or improve soil health and productive capacity while supplying numerous ecosystem services and agricultural products. In contrast, poor management can alter or eliminate grazingland vegetation, resulting in provision of fewer and poorer ecosystem services and less agricultural output. For instance, increasing stocking rates shifted North American midgrass communities, composed of a mixture of C3 and C4 grasses, to shortgrass communities dominated by C4 grasses (Launchbaugh, 1967; Hanson et al., 1978; Porensky et al., 2016). Concurrently, changing climates promise to impact grazinglands in novel ways.

Simulation models are useful for providing answers to alternative management and climate scenarios over long periods of time because it may be impossible or infeasible to conduct the large-scale research required to answer the same questions through field research. Many ecosystem models are capable of simulating grasslands, each with strengths and weaknesses. A few examples include: 1) the PHYGROW model (Stuth et al., 2003b), which has been used to anticipate forage shortages in grazinglands for over a decade (Stuth et al., 2003a; Stuth et al., 2005; Angerer, 2012); 2) GPFARM-Range, which has been used to simulate forage and cow-

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http://dx.doi.org/10.1016/j.ecolmodel.2017.02.004
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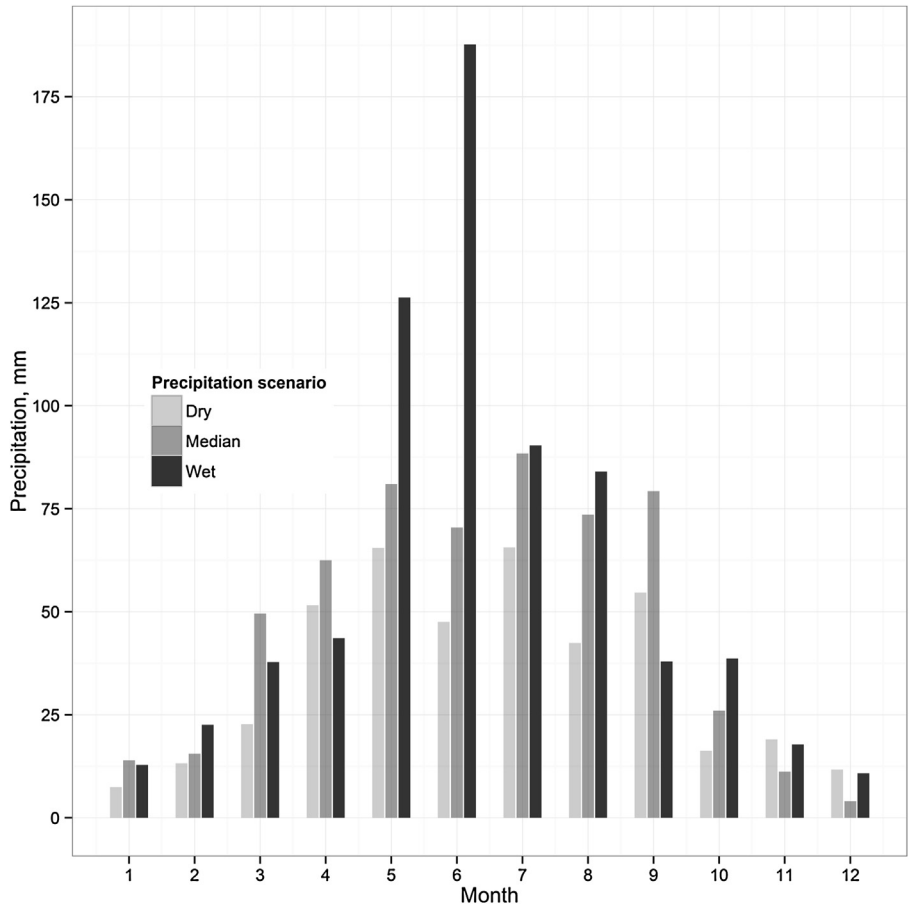

Fig. 1. Mean monthly precipitation at Hays, Kansas for the three scenarios: 1) median 5-year precipitation period since 1900 (1999–2003), 2) driest 5-year period since 1900 (1952–1956), and 3) wettest 5-year period since 1900 (1947–1951).

calf production in the Great Plains (Andales et al., 2005, 2006); SAVANNA (Coughenor, 1993), which includes spatial representation of ecosystem components; 4) the Sustainable Grazing Systems model (Johnson et al., 2003) which has been used to simulate forage production and steer liveweight gain in Australia (Doran-Browne et al., 2014); and 5) the APEX model (Gassman et al., 2010), a farm-scale version of EPIC (Williams et al., 1984). APEX has been in development for decades, has been extensively tested, and simulates production of a wide variety of crops and environmental variables. APEX and its related models (EPIC, ALMANAC, and SWAT) have been used to simulate perennial grass production (e.g., Kiniry et al., 2008; Wang et al., 2014; Santhi et al., 2001) but their development in this area is less mature than for annual crops.

Since 2003, APEX has been used by the Conservation Effects Assessment Project (CEAP) within the United States Department of Agriculture's Natural Resources Conservation Service to model the yield and environmental impacts of alternative farm conservation practices on croplands. In this capacity, the model helps to identify those conservation practices and suites of practices which are most effective at achieving desired environmental goals and the associated gain or loss of agricultural yield. To extend the use of APEX to rangeland and pastureland for the purposes of CEAP, it was necessary to enhance the model's ability to simulate grazing land dynamics. Specifically, the model required an improved ability to simulate perennial plant production throughout the entire year, improved competitive dynamics among plant species growing in mixture, and improved interaction between plant and animals. This study focuses on the first two requirements. Plant-animal interactions will be addressed by future work.

Therefore, we modified the APEX model (0806 version) to improve its ability to simulate perennial grassland vegetation. In the following sections, we: 1) describe the modifications made to the plant growth module, 2) conduct a sensitivity analysis and, 3) provide examples of the new model's performance with a historic dataset and hypothetical scenarios.

2. Methods

2.1. Plant growth module modifications

2.1.1. The APEX model

The APEX (Agricultural Policy/Environmental eXtender) model is a process-based model for simulating impacts of land management on whole farms and small watersheds. APEX is written in FORTRAN and uses a daily time step. Gassman et al. (2010) described the model's 12 major components, which include climate, hydrology, crop growth, pesticide fate, nutrient cycling, erosion-sedimentation, carbon cycling, management practices, soil temperature, plant environment control, economic budgets, and routing between land units. Climate inputs, including precipitation, daily maximum and minimum temperatures, relative humidity, and wind speed can be input from daily records or generated from monthly descriptive statistics. APEX is capable of simulating multiple species growing together in competition. Although species are defined by 60–70 different parameters, depending on the version of APEX, only a small subset of these (e.g., radiation use efficiency, maximum leaf area index) need to be adjusted for most model applications. Plant species compete for light, water, and nutrients.

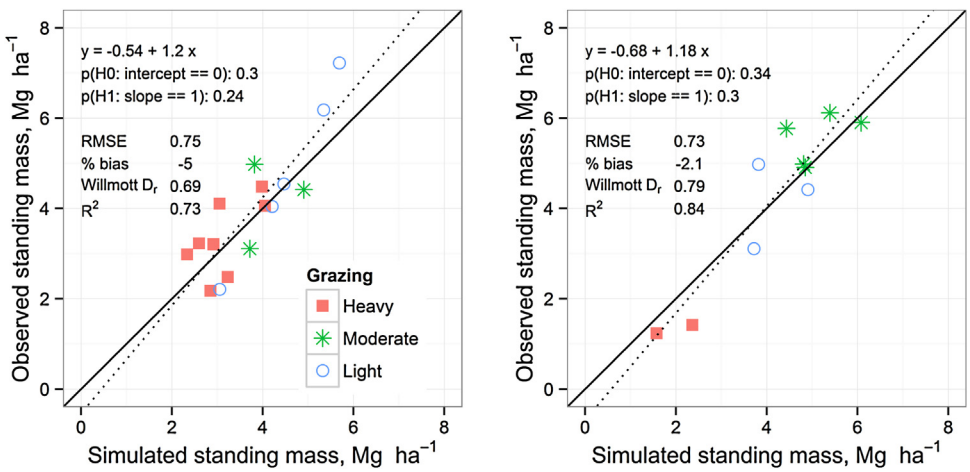

Fig. 2. Simulated vs. observed values of standing crop (Mg ha^{-1}) for the sum of all species in the calibration (left) and validation (right) sets. Each point represents a single clipping date (year). Colors and shapes indicate the grazing treatments. Values of root mean square error (RMSE), % bias, Willmott's D_r, and r^2 are displayed on the plot. The dotted line is the regression of observed values on simulated values. The equation for the regression is printed in the top left corner with the p-values for tests that the intercept is 0 and the slope is 1.

If the user inputs fewer than 10 soil layers, APEX can split them into 10 individual layers for simulation.

The EPIC and APEX models were originally designed for annual crop simulation, and although they have been used to model perennial crops (e.g., Tuppad et al., 2010; Kumar et al., 2011), perennial crops have never been the models' primary focus. Thus, to improve the simulation of functional processes on grazing lands, it was necessary to enhance APEX's ability to simulate perennial plant growth. However, while making modifications, we took care to minimize the impact on the models' primary historic use (i.e., simulation of annual crops).

2.1.2. Plant population curve

APEX0806 required that herbaceous plant population input values (PPL1 and PPL2) be stated in terms of number of plants m^{-2}. On grazing lands, grasses are more commonly described in terms of basal area, the percentage of the soil surface that is covered by the base of a plant. Expressing herbaceous plant population as basal area was technically possible in previous versions of APEX but was undocumented. The new version explicitly permits the user to choose between population (plants m^{-2}) or basal area (%) for each species. The model user can manually adjust the basal area or population during a simulation, but APEX does not automatically change basal area or population in response to environmental conditions.

2.1.3. Allocation of new biomass. APEX0806 simulated daily changes in plant biomass by adding the day's net change in biomass to the previous day's biomass and allocating the result to aboveground (STL – standing live, kg ha^{-1}) or belowground (RW – root, kg ha^{-1}) biomass pools. The portion allocated above or belowground was determined by the plant's growth stage, measured as an index of heat units (HUI), and the crop-specific parameters RWPC1 and RWPC2. Parameters RWPC1 and RWPC2 define the endpoints of a linear function that describes the portion of biomass that is allocated belowground (RF) at emergence (RWPC1; when HUI = 0.0) and maturity (RWPC2; when HUI = 1.0):

$$RF_i = (1\text{-}HUI_i) * RWPC1 + HUI_i * RWPC2$$

In other words, RF shifts from RWPC1 to RWPC2 as the plant matures throughout the growing season.

Experiments have shown that plant growth patterns work to bring the root:shoot ratio back into equilibrium after a defoliation event (Gregory, 2006). A small amount of biomass can be transferred from storage organs to produce aboveground regrowth of perennial species, but this transfer has a very limited duration (White, 1973; Morvan-Bertrand et al., 1999). However, the APEX0806 implementation of biomass transfer was virtually unrestricted in time or quantity. This was potentially problematic for crops that could be harvested repeatedly, whether by grazing animals or mechanical equipment, because the model would reallocate biomass unrealistically following these harvest events. Thus, we restricted biomass transfer to occur only when 3 conditions are met:

a LAI < (0.03 * Maximum possible LAI), and
b Air Temperature > Base Temperature, and
c the plant has not yet reached maturity during the current growing season,

where LAI is leaf area index (m^2 m^{-2}), Air Temperature (°C) is the mean of the daily maximum and minimum temperatures, and Base Temperature (°C) is the minimum air temperature required for the species to grow. The constant 0.03 in criteria #1, above, was determined after running the model with several different values. We determined 0.03 to be a conservative value that typically restricts transfer to a reasonable period of days to weeks. The exact duration of transfer depends on climate conditions and the rate at which the leaf area of a species develops. To control the quantity of biomass transferred from belowground to aboveground, we added a new, unitless parameter (belowground to aboveground transfer ratio weighting coefficient; R2SC) that ranges from 0 to 1 and remains constant for the duration of the simulation. When R2SC is 0 the model performs as in APEX0806, with all biomass partitioned between belowground and aboveground fractions on a daily basis according to belowground fraction parameters RWPC1 and RWPC2. When this value is 1, no transfer of biomass from belowground to aboveground is permitted. Values between 0 and 1 use a weighted average of both approaches. Thus, high values of this parameter (e.g., 0.95) allow a small transfer of biomass from belowground to aboveground, such as in the spring when plants begin growth.

We also modified the code to address the situations when the three criteria for biomass transfer were not met, which constitutes the majority of the year. With the modification, each day's biomass growth (the result of the day's photosynthesis) was allocated belowground and/or aboveground, but the previously existing biomass was not reallocated. With this approach, RWPC1

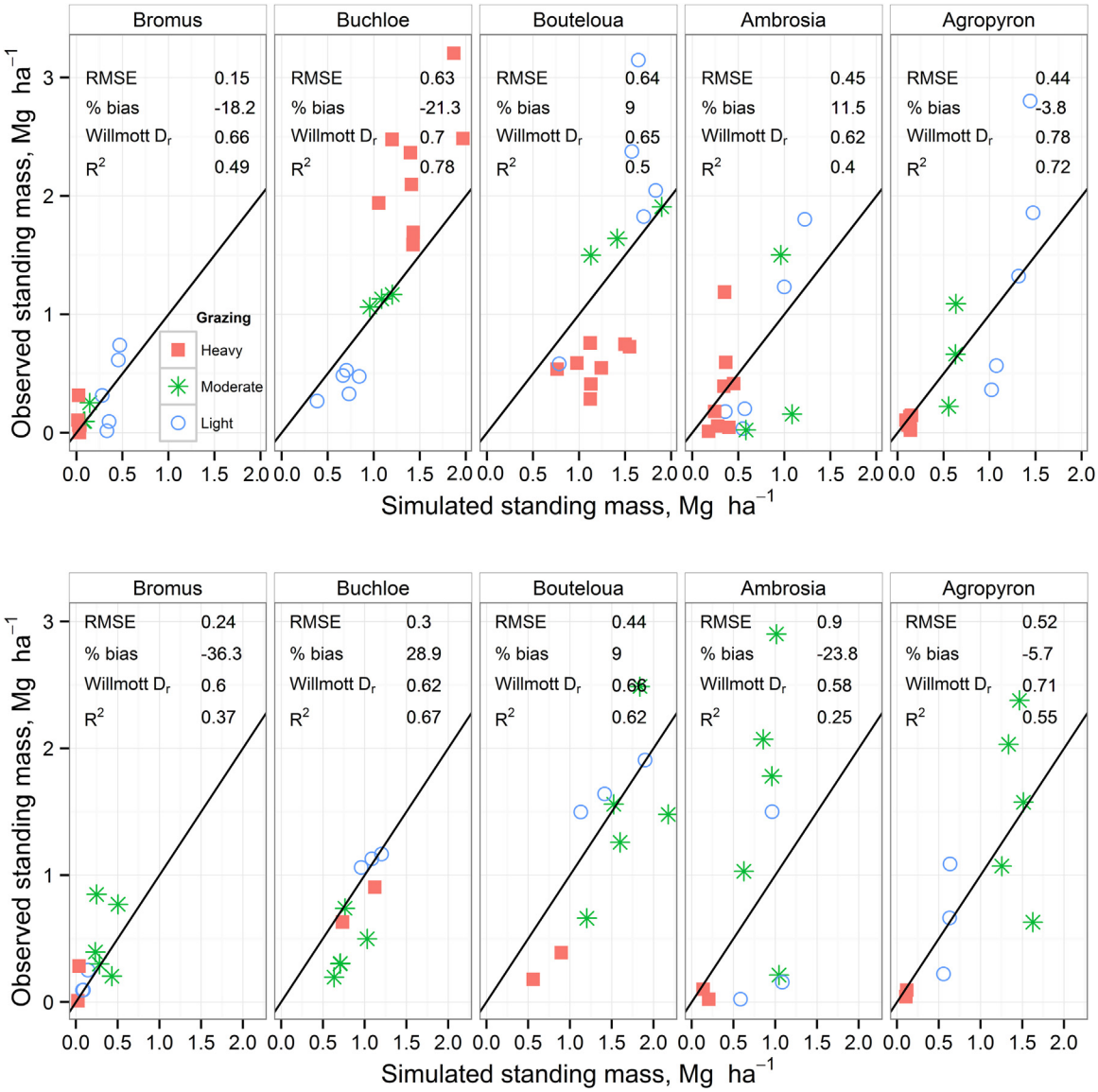

Fig. 3. Simulated vs. observed values of standing crop (Mg ha^{-1}) for each of 5 species *Bromus arvensis*; *Buchloe dactyloides*; *Bouteloua gracilis*; *Ambrosia psilostachya*; *Agropyron smithii*) in the calibration (upper) and validation (lower) sets. Each point represents a single clipping date. Colors and shapes indicate the grazing treatments. Values of root mean square error (RMSE), % bias, Willmott's D_r, and r^2 are displayed on the plot.

and RWPC2 become targets as to how much biomass should be allocated belowground rather than absolute requirements. In practice, this means that after harvesting a plant's aboveground biomass, it will have a higher current belowground biomass:total biomass ratio than what RWPC1 and RWPC2 would suggest for the current stage of maturity. Thus, new biomass will be preferentially allocated aboveground to bring the current belowground biomass:total biomass ratio towards agreement with the target ratio (Gregory, 2006) determined by RWPC1 and RWPC2 according to the following:

$$RFDF_i = (RW_i/DM_i)\text{-}RF_i$$

$$RF2_i = 1 \qquad \text{when } RFDF_i <= -0.02$$

$$RF2_i = RF_i \qquad \text{when } -0.02 < RFDF_i < 0.02$$

$$RF2_i = 0 \qquad \text{when } RFDF_i => 0.02$$

$$RW_i = RW_{i-1} + RF2_i * RGD_i$$

Where RFDF is the difference between the current belowground to total biomass allocation and the target allocation, RF is the desired belowground fraction determined by HUI, RW (kg ha^{-1}) is belowground biomass, DM (kg ha^{-1}) is dry matter of all above and belowground plant parts, RF2 is the fraction of the day's biomass that is allocated belowground (bounded by 0 and 1), RGD (kg ha^{-1}) is the day's increase in biomass, and i indicates the day. The threshold value of ± 0.02 in the above criteria assures that when a plant's belowground to total biomass ratio is out of agreement with the target by more than 2%, the plant will quickly approach its target ratio by allocating 100% of new photosynthate either above or belowground, assuming growing conditions are adequate to produce new biomass. With these changes it also became necessary to increase root senescence throughout the year because RW could

not decrease without belowground harvesting. Daily loss of belowground biomass (RWLOSS, kg ha^{-1}) was calculated as:

$$RWLOSS_i = RDEAT * RW_i$$

RDEAT is set to 0.0015 by default, but can be modified for individual crops. The 0.0015 rate results in remaining live belowground percentages for a given age cohort of 58% after 1 year, 33% after 2 years, and 19% after 3 years, if no additional roots are grown. In comparison, Weaver (1958) found 66% of young little bluestem roots alive after 2 years and just 10% alive after 3 years. Weaver (1958) also found no death of big bluestem roots after 2 years and that 80% were still alive after 3 years.

2.1.4. Water stress and competition for water

It has been shown that herbaceous plants adjust their belowground biomass:total biomass ratios in response to environmental stress, including water stress (WS; Poorter et al., 2012). To capture this effect, we modified the target belowground biomass:total biomass ratio (RF) according to the following, when HUI > 0.3:

$$RF_i = RF_i * (1.1 - 0.1 * WS_i)$$

Because WS ranges from 0 to 1, this results in a maximum change in the belowground biomass:total biomass ratio of 10%, which is approximately the maximum change due to water stress found by Poorter et al. (2012). Thus, the definitions of RWPC1 and RWPC2 have been modified slightly to be the target proportion of biomass that is belowground when the plant is not under water stress.

APEX0806 allowed equal access to water contained in a soil layer for all species with live roots present in a soil layer, depending on species demand. On successive days, the species would alternate which had the first opportunity to extract soil water to fill its water demand. The species with earlier access on a given day could extract as much water as it demanded or was available. If available water remained for the next species, it could also extract water. We revised this so that the biomass of the root system present in the soil layer became a factor in the competition for water. That is to say, the species with more root biomass in a given soil layer is able to preferentially extract available soil water under water-limited conditions according to the relative belowground biomass in a soil layer on a given day, as follows:

$$RWF_{lc} = \exp((RWT_{lc}\text{-}RWT_l)/RWT_l)$$

Where RWT_{lc} (kg ha^{-1}) is the live mass of crop c in layer l, and RWT_l is the sum of live mass from all crops in soil layer l. Water use for each soil layer is calculated using the original APEX compensation approach and adjusted with RWF.

2.1.5. Maturity and regrowth of herbaceous perennials

When an herbaceous perennial plant reaches maturity in the field, where maturity is defined as having set viable seed, much of its leaves have senesced or will soon senesce. However, leaf retention and even regrowth are also common if environmental conditions are suitable. In APEX, HUI is reset to 0 when plants reach maturity (indicated by an HUI value of 1.0), but in APEX 0806, reaching maturity did not cause a change in LAI and STL. Resetting HUI had the effect of virtually converting the old leaves and standing mass into fresh growth. Consequently, LAI and STL continued to increase after maturity if growing conditions were adequate. To more accurately simulate gradual senescence observed in the field, we modified APEX so that biomass and leaf area produced before maturity would gradually decline after maturity. The revised rate of STL loss (LOSS_STL, kg ha^{-1}) for crop C followed the same function as in version 0806, with the exception of changing the value of X in the following equation.

$$LOSS_STL_c = 0.01 * (HUI_c + X)^{10}$$

Previously, X was a constant 0.01 (APEX 0806) that assured the base of the power function was greater than 0. Now, X is 0.01 until a plant reaches maturity, at which time X is 1.0 for STL produced up until that time, and X is 0.01 for STL regrowth produced after reaching maturity. Because HUI_c is reset to 0 at maturity, setting X to 1.0 at maturity will maintain a relatively rapid rate of STL loss once maturity is reached. Before a crop has reached maturity, LAI gain or loss is calculated as in APEX0806. After reaching maturity, loss of LAI is calculated by:

$$X1 = LOG_{10}((1.0 - HUIM_c)/(1\text{-}DLAI_c))$$

$$RTO = RLAD_c * X1$$

$$LAINEW_c = LAID_c * 10^{RTO}$$

$$LOSS_LAI_c = LAI_{c,i\text{-}1} - LAINEW_c$$

Where $HUIM_c$ is 0.95 if crop c has reached maturity or HUI_c otherwise, $LAID_c$ (m^2 m^{-2}) is LAI_c when HUI_c reached the point of maturity at which LAI_c began to decline ($DLAI_c$, m^2 m^{-2}). $LAI_{c,i\text{-}1}$ is the LAI of crop c from the previous day. X1 has a lower bound of −5. RTO has a lower bound of −10. This equation reduces LAI_c until the pool of LAI_c produced before maturity goes to 0.

Simultaneously with losses of LAI and STL, new growth of LAI and STL remain possible and unchanged from version 0806. As a result, the net change in LAI and STL after maturity depends upon the balance between additions and subtractions of LAI and STL.

Finally, we observed that the default parameter values of some perennial herbaceous species, found in the APEX crop table, were more appropriate for annuals than perennials. This problem has previously been noted by others (Zhang et al., 2011). In particular, it has been shown that the proportion of biomass allocated belowground by herbaceous perennial grassland species commonly exceeds that allocated aboveground, and may be 4 or more times greater, especially in arid grasslands (French et al., 1979). Thus, we increased RWPC1 and RWPC2 to 0.90 and 0.65 for perennial grasses, respectively, rather than the default values of 0.40 and 0.20 (Table 1). At maturity the actual belowground to aboveground biomass ratio could diverge from 0.65 due to harvest events or environmental conditions, especially drought. These values may need to be adjusted for simulations of different perennial species or growing conditions. Because radiation use efficiency (WA) values in the crop table are often determined by measuring aboveground biomass and making assumptions about belowground mass, it was necessary to adjust WA as well. The complete crop table and all input files used in our simulations are available at Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.h3fj0.

2.2. Field site

In order to evaluate the performance of the updated model, we used a long-term (1946–1965) grazing experiment at Hays, Kansas (38.87 N, 99.31 W) that evaluated vegetation and animal performance (Launchbaugh, 1957, 1967). Soils were Harney silt loams with 0–3% slopes, and Harney-Carlson silt loams with 0–3% slopes, both corresponding to the Loamy Upland ecological site in Major Land Resource Area 73 (USDA NRCS, 2006). Average annual precipitation (1868–1961) was 582 mm, 77% of which fell from April through September (Albertson and Tomanek, 1965). Experimental pastures were typically grazed from May 1 to Oct. 1 or Nov. 1

Table 1
Parameter values for the five species used to simulate Hays, Kansas plant communities. Parameter descriptions are followed by their variable name in the APEX model, in parentheses. Values were determined by first using published literature and expert opinion as guides, followed by manual calibration. Complete input files are available at Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.h3fj0.

Literature sources		Weaver and Zink (1946); Sims and Singh (1978); French et al. (1979)	Weaver and Zink (1946); Dahlman and Kucera (1965)	Weaver (1958); Vermeire et al. (2017); Vermeire et al. (no date)	Kiniry et al. (1995, 2002, 2007, 2014)	Frank and Bauer, (1991); Kiniry et al. (1995, 2007); He et al. (2007); Kiniry et al. (2014)	Detling (1979); Kiniry et al. (2002)	
Species	Belowground biomass: aboveground biomass at emergence (RWPC1)	Belowground biomass: aboveground biomass at maturity (RWPC2)	Daily portion of roots that die (RDEAT)	Rooting Depth, m (RDMX)	Radiation use efficiency, g * $(10\,MJ)^{-1}$ (WA)	Maximum leaf area index (DMLA)	Optimum temperature, C (TOP)	Base temperature, C (TBS)
Bouteloua gracilis	0.90	0.65	0.0015	0.7	16	1.5	25	8
Buchloe dactyloides	0.90	0.65	0.0015	0.8	10	1.5	25	10
Agropyron smithii	0.90	0.65	0.0015	1.5	16	2.5	15	3
Bromus arvensis	0.60	0.30	0.0015	0.5	25	2.0	12	0
Ambrosia psylostachia	0.90	0.30	0.0015	1.5	15	1.5	17	10

by yearling steers or heifers, although grazing was sometimes terminated early when forage was inadequate (Launchbaugh, 1967). Three stocking rates were used: light, moderate, and heavy (2.0, 1.4, and 0.81 ha animal^{-1}, respectively). Total basal cover and basal cover by major species (blue grama [*Bouteloua gracilis*], buffalograss [*Buchloe dactyloides*], and western wheatgrass [*Agropyron smithii]*) were recorded in 1946, 1949, and 1955–1965. Grazing exclosures in each pasture were moved annually. Vegetation in exclosures was clipped and weighed by species (*Buchloe dactyloides*, *Bouteloua gracilis*, *Agropyron smithii*) or group (annual grasses, weeds) at the end of each grazing season from 1956 to 1965. These data were published in figures by Launchbaugh (1967) and we digitized them using Plot Digitizer 2.6.6 (Huwaldt and Steinhorst, 2014).

We simulated the Hays site using a Harney soil and weather data (temperature and precipitation) from Hays, Kansas (NOAA, 2015). To simulate the effects of grazing followed by establishment of an exclosure, we ran the model once for each year of available exclosure data. The simulations were initiated in 1936, which allowed the model to run for at least 10 years before available field measurements. The 10 years allowed a spin-up period for soil pools (e.g., carbon and nitrogen) to equilibrate prior to the evaluation period. Then, for each year of available data, the model continued with annual grazing following the actual grazing dates given by Launchbaugh (1967) until the year in which data was collected from an exclosure. In the year of data collection, grazing was not simulated.

The Hays dataset included 30 treatment-years for "forage production," which is modeled as the sum of STL (standing live aboveground biomass, kg ha^{-1}) and standing dead aboveground biomass (STD, kg ha^{-1}). Based on aboveground biomass (STL + STD), we split the treatment-year combinations into 5 quantiles with 6 combinations in each. Within each quantile, 4 of the 6 were randomly selected for calibration and the other 2 were used for validation. Calibration and validation were carried out at the same grouping level at which the data was collected (*Buchloe dactyloides*, *Bouteloua gracilis*, *Agropyron smithii*, annual grasses, or weeds). Thus, for each year x treatment combination, there were 15 data values (5 plant types x 3 treatments).

Parameter values were based on published literature or expert opinion and simulations were calibrated manually (Table 1). The three grazing intensities were simulated with identical input files except for: 1) differences in stocking rate, 2) density of individual plant species, and 3) daily standing dead fall rate coefficient (parameter #76) converting standing dead material to flat residue. Our evaluation of Launchbaugh's (1967) data showed weak evidence for correlation between basal area at the end of one year and aboveground biomass of a given species in the following year. APEX does not automatically simulate changes in basal area, so for perennial grasses, we ran the simulation with the mean basal area recorded by Launchbaugh (1967) for each species over the period 1956–1965. For the annual grass Japanese brome [*Bromus arvensis*] and for weeds, which were represented in the simulation by the dominant species, western ragweed [*Ambrosia psylostachia*], we estimated basal values because measurements were not reported by Launchbaugh (1967). We calculated daily fall rate as 0.0054 for light and moderate stocking and 0.0075 for heavy stocking by using the observed 365-day rate (Launchbaugh, 1967). Evaluation of fit was conducted with calculation of percent bias, Wilmott's D_r (Willmott et al., 2012), and r^2. We calculated fit statistics for aboveground biomass on Oct. 1 for all three stocking rates as a group. We calculated fit statistics for each stand as a whole (sum of all plant species) and for each individual species.

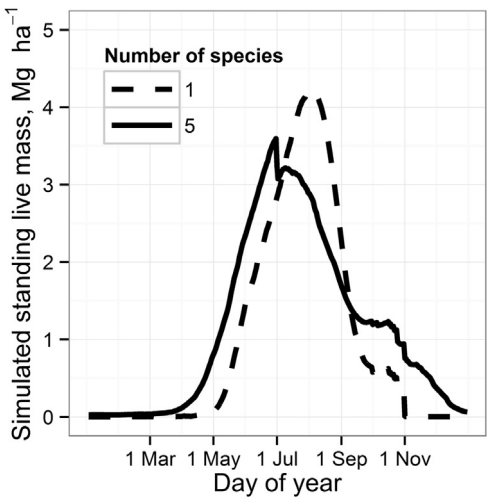

Fig. 4. Mean daily standing live biomass (Mg ha^{-1}) over 10 years for the light stocking rate treatment simulated with a suite of 5 species (solid line) or a single species (dashed line).

2.3. Sensitivity analysis

We evaluated the revised model and the new parameters by conducting independent sensitivity analyses in several areas. For the sensitivity analyses, we simulated the Hays, Kansas field site without grazing.

2.3.1. Allocation of new biomass

Belowground mass and standing live mass were evaluated throughout the year to compare vegetation removal scenarios (i.e., with or without cutting hay that removes 85% of the standing biomass on June 15). We varied R2SC for each scenario, using values of 0, 0.95, and 1.0, resulting in 6 total scenarios (2 cutting frequencies x 3 parameter values). We chose 0 and 1 to represent the extremes for this parameter and 0.95 based on our own experimentation with the model.

2.3.2. Water stress

To evaluate the sensitivity of belowground biomass:total biomass ratios to water stress, we ran three scenarios including the two dominant species, *Agropyron smithii* and *Bouteloua gracilis*. Our three scenarios were based on the driest (1952–1956; 418 mm mean annual precipitation; hereafter "dry" scenario), median (1999–2003; 575 mm mean annual precipitation; hereafter "median" scenario), and wettest (1947–1951; 710 mm mean annual precipitation; hereafter "wet" scenario) 5-year periods from from 1900 to 2014 (Fig. 1). The actual median value was 574.9 mm year^{-1} which occurred from 1955 to 1959. However, this 5-year period included the driest year on record and four relatively wet years; thus, we used the period from 1999 to 2003, which included 5 non-extreme years and a mean of 575.4 mm year^{-1}. Scenarios were run with weather from 1936 to 1946 to provide identical initial conditions, followed by weather for the particular scenarios. We set variable R2SC to 1.0, and we report the belowground biomass:total biomass ratios and standing live biomass for the final 5 years of each scenario.

2.3.3. Interspecific competition for water

To evaluate interspecific competition for water, we simulated growth of two identical deep-rooted species (*Bouteloua gracilis*) together, or one deep-rooted and one shallow-rooted species under the three previously described weather scenarios. Plant parameters for these species were identical except for rooting depth, which was 1.0 m or 0.2 m. We selected these rooting depths because: 1) they are far enough apart to be in different simulated soil layers, a necessary condition for obtaining differences in simulation results; and 2) neither reaches the water table, which would interfere with our test of response to different precipitation conditions. Simulation results were evaluated by analyzing standing live mass, belowground mass, and belowground mass distribution by depth.

2.3.4. Single species simulation

We examined the feasibility of running a simulation with a single species rather than a suite of species. To do this, we repeated the simulations described above in section 2.2 with the following changes: 1) a single species, *Bouteloua gracilis*, was used for the simulation; 2) the radiation use efficiency of the species was increased from 16 to 20 g * (10 MJ)$^{-1}$; and 3) we increased the population/basal area of the single species to be the sum of all species from the 5-species simulation. Thus, the modeled "species" was no longer intended to represent *Bouteloua gracilis*, but rather the suite of species present at the site.

2.4. Model application

To demonstrate the utility of the model we devised a simple but relevant application—the impact of increasing stocking rate on residual standing biomass and supplemental feeding. For this demonstration we used the same model settings as for the moderate stocking rate scenario, except for: 1) varying the stocking rate across a range from 0.4 to 4.0 ha animal^{-1}, and 2) varying the grazing efficiency. Grazing efficiency is the fraction of forage that is consumed by livestock divided by the quantity of forage that disappears due to all activities (e.g., weathering, trampling, consumption by insects or wildlife (Smart et al., 2010)). Grazing efficiency increased linearly from approximately 35% up to 65% as grazing pressure increased at Hays (Smart et al., 2010). The values from Smart et al. (2010) do not perfectly correspond to the APEX grazing efficiency parameter because APEX already incorporates a "fall rate" from standing dead biomass to the litter biomass pool. Therefore, across our range of simulations we applied the following equation to determine the grazing efficiency parameter:

$$\text{Grazing efficiency} = 70\% \quad \text{when stocking rate heavier than } 0.8\ \text{ha animal}^{-1}$$

$$\text{Grazing efficiency} = 90\% - (25\% * \text{stocking rate}) \quad \text{when } 0.8\ \text{ha animal}^{-1} < \text{stocking rate} < 2.0\ \text{ha animal}^{-1}$$

$$\text{Grazing efficiency} = 40\% \quad \text{when stocking rate lighter than } 2.0\ \text{ha animal}^{-1}$$

We report two of the model outputs, 1) the sum of standing live and standing dead mass on Oct. 1 ("residue"), and 2) the amount of supplemental hay required to meet animal intake demands. When standing forage is insufficient to meet animal demands, based on the total digestible nutrients of the animals' diet (NRC, 2000), the model automatically supplies hay with a total digestible nutrient value of 50%.

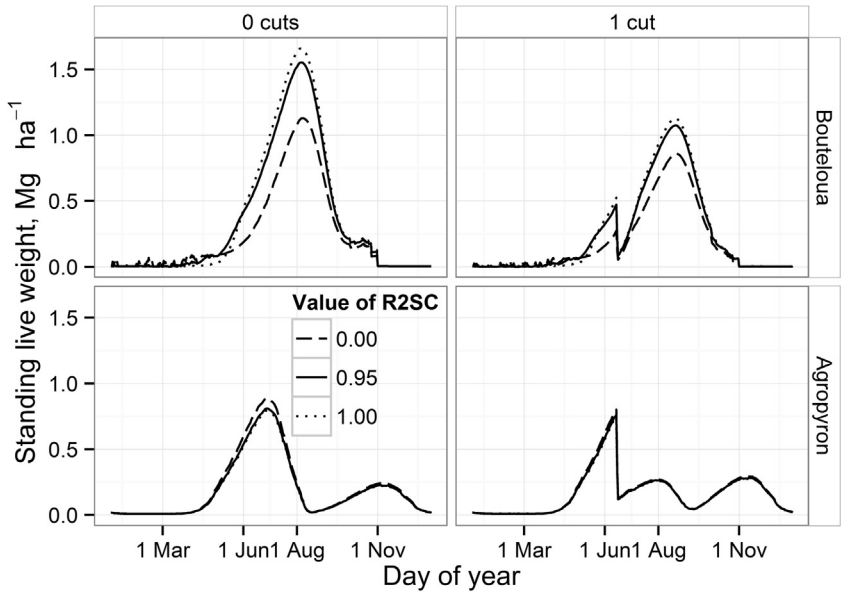

Fig. 5. Sensitivity analysis of R2SC. The figure shows daily simulated standing live mass (Mg ha^{-1}) at Hays, Kansas for three values of the parameter. Five species were simulated but only *Bouteloua gracilis* and *Agropyron smithii* are shown for clarity. Values are means of 10 years (1956–1965) with no harvest (left) or 1 annual harvest on June 15 (right).

3. Results

3.1. Field site

In the calibration data set, simulated and observed standing crop biomass had an r^2 of 0.73 and Willmott's D_r of 0.69 (Fig. 2). Both statistics improved in the validation dataset, resulting in values of 0.84 and 0.79, respectively (Fig. 2). Across all years and treatments, mean and standard deviation of standing crop biomass were 3.9 (1.1) for the simulated values and 4.0 (1.5) for the observed values in the calibration dataset. In the validation dataset, the values were 4.2 (1.4) and 4.3 (1.8), respectively. Fit statistics were generally lower for individual species than the group as a whole in both the calibration and validation datasets (Fig. 3). Values of r^2 ranged from 0.40 to 0.78 in the calibration dataset, with a mean of 0.58. Willmott's D_r had a narrower range, from 0.62 to 0.78 and a mean of 0.68. The validation dataset was similar with an r^2 range from 0.25 to 0.67 and a mean of 0.49. The validation dataset's Willmott's D_r ranged from 0.58 to 0.71 with a mean of 0.63. No single species clearly outperformed the others when considering both fit statistics and both datasets.

Simulating the field site using a single species (Fig. 4) resulted in similar values of r^2 (0.64) and Willmott's D_r (0.69) as when we used the suite of 5 species for the calibration dataset, and percent bias was just 5%. However, the performance against the validation set was worse when using a single species, resulting in r^2 of 0.45 and Willmott's D_r of 0.61. In both the calibration and validation datasets, simulation with a single species tended to overestimate the heavy grazing treatment and underestimate the light grazing treatment, but the overall percent bias was just −0.5% for the validation.

3.2. Sensitivity analysis

Sensitivity to adjustments in R2SC (belowground to aboveground transfer ratio weighting coefficient) varied by plant species. Both *Buchloe dactyloides* and *Bouteloua gracilis* standing live mass (Fig. 5) and belowground mass (not shown) were relatively sensitive to changes in the parameter when it was adjusted from 0 to 1.0. In contrast, *Agropyron smithii* (Fig. 5) and *Bromus arvensis* were very insensitive, with *Ambrosia psilostachya* intermediate. Simulated belowground biomass:total biomass ratios were near 1.0 when growth initiated in spring, before moving closer to the target belowground biomass:total biomass ratio as growth accelerated (Fig. 6). When aboveground biomass was cut on June 15, the simulated belowground biomass:total biomass ratio rose to near 1.0 once again. The subsequent response depended upon species. *Agropyron smithii*, a C3 grass that was near maturity and not well adapted to growing under hot conditions, did not produce enough new biomass to bring its simulated belowground biomass:total biomass ratio nearer its target ratio (Fig. 6). In contrast, *Bouteloua gracilis*, a C4 grass that was still experiencing rapid growth on June 15, quickly moved its belowground biomass:total biomass ratio into closer agreement with the target by preferentially allocating

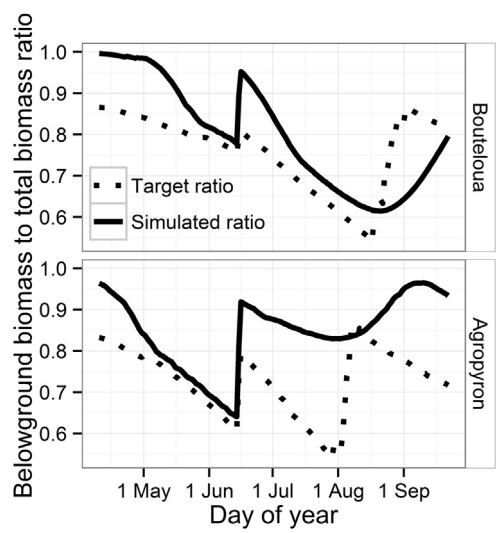

Fig. 6. The simulated belowground biomass:total biomass ratios of a C4 grass, *Bouteloua gracilis* and a C3 grass, *Agropyron smithii*, when cut for hay on June 15. The solid line is the simulated ratio of belowground biomass:total biomass and the dotted line is the target ratio determined by accumulated heat units. R2SC was set to 1.00. Only two plant species are shown for simplicity but five were included in the simulation.

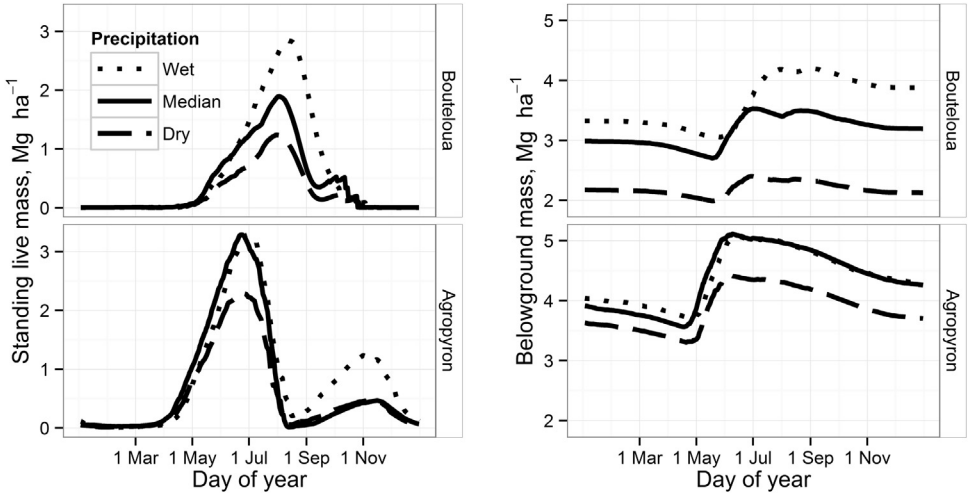

Fig. 7. Simulated daily values of aboveground live mass (Mg ha^{-1}, left) and belowground mass (Mg ha^{-1}, right) of *Bouteloua gracilis* and *Agropyron smithii* throughout the year, averaged across 5 years. Three scenarios were run, using: 1) median 5-year precipitation period since 1900 (solid line), 2) driest 5-year period since 1900 (dashed line), and 3) wettest 5-year period since 1900 (dotted line).

new biomass aboveground rather than belowground after being cut (Fig. 6). Fig. 6 also depicts the increase in the target belowground biomass:total biomass ratio in late summer when the plants reached maturity.

Belowground mass and standing live mass of *Agropyron smithii* and *Bouteloua gracilis* responded to changes in annual precipitation; the dry scenario affected biomass more than the wet scenario, relative to median precipitation (Fig. 7). Mean daily water stress values (where 0 represents extreme stress and 1 represents no stress) for *Bouteloua gracilis* and *Agropyron smithii*, respectively, for the three scenarios were 0.53 and 0.68 (dry), 0.76 and 0.81 (median), and 0.74 and 0.86 (wet). Belowground biomass:total biomass ratios of both species were also sensitive to changes in precipitation (see Fig. S1 in the online version at DOI: http://dx.doi.org/10.1016/j.ecolmodel.2017.02.004). Averaged across years, the mean annual minimum belowground biomass:total biomass ratios for the three scenarios were approximately 0.65 (dry), 0.62 (median), and 0.60 (wet).

When two versions of *Bouteloua gracilis* were grown together, one deep-rooted (max depth 1.0 m) and one shallow-rooted (max depth 0.2 m), the shallow-rooted version maintained greater root biomass in the upper soil layers (to a depth of 0.3 m) but the deep-rooted version had greater total belowground biomass (Table 2) and aboveground biomass (data not shown). Belowground biomass of both shallow- and deep-rooted species increased with precipitation, but whereas the shallow-rooted species increased by 86% from the dry to wet scenarios, the deep-rooted species only increased 39%.

In addition to growing one shallow-rooted and one deep-rooted *Bouteloua gracilis* together, we also grew two deep-rooted *Bouteloua gracilis* together. Rooting depth pairing had little influence on total grassland aboveground biomass under the dry and median precipitation scenarios (Table 3). However, under the wet precipitation regime, 2 deep-rooted species were better able to exploit the additional moisture and produced more aboveground biomass than 1 deep and 1 shallow species. Root distribution was mediated by whether the competing species was shallow- or deep-rooted (Table 4). When competing with a shallow-rooted species, the deep-rooted species concentrated a greater percentage of its belowground biomass below the root zone of the shallow-rooted species.

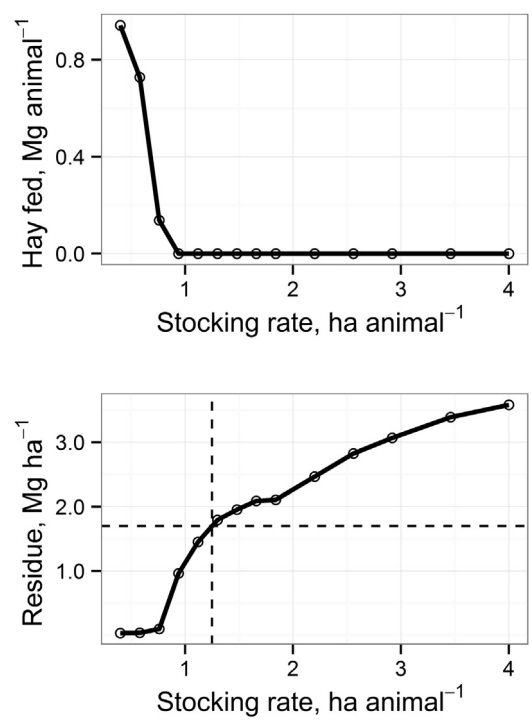

Fig. 8. Results of simulating a variety of stocking rates at Hays, Kansas. Steers grazed continuously from May 1 to Oct. 1 of each simulated year. Plots show the mean annual simulated values for each stocking rate from 1956 to 1965. When standing forage was insufficient to meet animal demands, supplemental hay was provided (upper figure). Residue (lower figure) is the sum of standing live and standing dead vegetation on Oct. 1 of each year. Dotted lines indicate the recommended minimum residue level (1.7 Mg ha^{-1}).

3.3. Model application

Across stocking rates ranging from very heavy (0.4 ha animal^{-1}) to very light (4.0 ha animal^{-1}) the model performed as theory suggests. Standing residue, including both live and dead material on Oct. 1, increased as stocking rate became lighter (Fig. 8). Standing residue approached 0 at a stocking rate of 0.76 ha animal^{-1} and hay was fed to supplement steers' diets. Compared with the measurements of Launchbaugh (1967), the model slightly underestimated

Table 2
Simulated belowground mass (Mg ha^{-1}) of deep-rooted and shallow-rooted C4 grasses grown together. Masses are shown for Oct. 1 in the final year of each simulation. Three scenarios were run, using: 1) median 5-year precipitation period since 1900, 2) driest 5-year period since 1900, and 3) wettest 5-year period since 1900.

Soil depth (m)	Dry (mean 418 mm yr^{-1})		Median (mean 575 mm yr^{-1})		Wet (mean 710 mm yr^{-1})	
	Rooting depth		Rooting depth		Rooting depth	
	Deep	Shallow	Deep	Shallow	Deep	Shallow
0–0.30	0.95	1.62	1.20	2.16	1.84	3.02
0.30–1.52	1.83	0.00	2.25	0.00	2.03	0.00
0–1.52	2.78	1.62	3.46	2.16	3.87	3.02

Table 3
Simulated aboveground and belowground live biomass (Mg ha^{-1}) for a grassland with one shallow-rooted and one deep-rooted C4 grass, or two deep-rooted C4 grasses, averaged over 5 years. Daily values of all species were summed on each day of the simulation, then daily values were averaged across 5 years of simulations, and finally the maximum mean daily value was determined. Three scenarios were run, using: 1) median 5-year precipitation period since 1900, 2) driest 5-year period since 1900, and 3) wettest 5-year period since 1900.

Rooting depth	Dry (mean 418 mm yr^{-1})	Median (mean 575 mm yr^{-1})	Wet (mean 710 mm yr^{-1})
		Aboveground biomass	
1 deep, 1 shallow	2.6	3.8	4.3
2 deep	2.8	3.7	5.3
		Belowground biomass	
1 deep, 1 shallow	4.4	5.8	6.0
2 deep	5.6	7.5	8.0

Table 4
Simulated belowground mass (Mg ha^{-1}) of a deep-rooted C4 grass when grown with a shallow-rooted species (shallow-rooted species not shown) or with a second, identical deep-rooted species. Masses are shown for Oct. 1 in the final year of each simulation. Three scenarios were run, using: 1) median 5-year precipitation period since 1900, 2) driest 5-year period since 1900, and 3) wettest 5-year period since 1900.

Soil depth (m)	Dry (mean 418 mm yr^{-1})		Median (mean 575 mm yr^{-1})		Wet (mean 710 mm yr^{-1})	
	Rooting depth of competing species		Rooting depth of competing species		Rooting depth of competing species	
	Deep	Shallow	Deep	Shallow	Deep	Shallow
0–0.30	1.34	0.95	1.89	1.20	2.79	1.84
0.30–1.52	1.19	1.83	1.53	2.25	1.92	2.03
0–1.52	2.52	2.78	3.42	3.46	4.71	3.87

the Oct. 1 residue for the lightest and heaviest stocking rates and slightly overestimated residue for the moderate stocking rate.

4. Discussion

4.1. Model sensitivity

Sensitivity to the updates made to the APEX model varied by species. The C4 grass, *Bouteloua gracilis*, was more sensitive to changes in the belowground:aboveground transfer parameter, likely because of its sensitivity to frost (Fig. 5). When large transfers were allowed from belowground to aboveground, much of the transferred material was killed by spring frosts. In contrast, the C3 grass, *Agropyron smithii*, also transferred biomass from belowground to aboveground in the spring, but the aboveground biomass was not killed by frost due to greater cold tolerance.

Changes in precipitation and rooting depth of competing species caused simulated plants to alter the distribution of their rooting mass to take advantage of available moisture (Tables 2 and 4). As precipitation increased, the shallow-rooted species benefited more than the deep-rooted species (Table 2). This matched expectations, as the deep-rooted species could access moisture that was inaccessible to the shallow-rooted species, assuming drought did not push soil moisture below the wilting point in the deep rooting zone. Overall, the model's sensitivity to interactions between weather and species attributes was encouraging for its application to alternative climate and vegetation scenarios.

4.2. Application, management, and future work

Our results of modeling the vegetation community using a single simulated species (Fig. 4) might be improved by making more adjustments to the crop parameters; we only changed the radiation use efficiency and the basal area. However, although simulated values of peak standing crop may differ little whether using one or many species for the simulation, it is also likely that simulating with a single species rather than 5 will less accurately simulate seasonal growth dynamics and forage quality, both of which are important for accurate simulation of plant-herbivore interaction. For instance, simulation using a single C4 grass suggested standing live biomass would not reach 1 Mg ha^{-1} until approximately June 1, whereas the simulation using 5 species reached this threshold in early May (Fig. 4). Furthermore, as simulation of inter-specific competition is improved in the APEX model, long-term vegetation dynamics would not be captured by a single-species simulation.

APEX does not automatically simulate changes in plant populations or basal area. The field site that we chose to simulate at Hays, Kansas experienced fluctuations in basal area and population over the 10 years of our simulation, particularly for *Buchloe dactyloides* and *Ambrosia psylostachia* (Launchbaugh, 1967). We ran our simulations using the mean observed basal area for each species. If APEX was able to simulate changes in basal area and plant population by species, it might better capture the inter-annual dynamics of biomass production at the level of the species and the entire stand. Even if APEX included this feature, it would likely remain much more difficult to accurately simulate the individuals within a suite

of noncultivated species growing in competition with one another, as compared to cultivated crops that have little genetic diversity and are grown in near monocultures. The challenge of simulating a suite of rangeland species was also noted in successive versions of the SPUR model; on several occasions, vegetative production of certain individual species was accurate while simultaneous simulation of particular competing species remained difficult (Carlson and Thurow, 1996; Foy et al., 1999; Pierson et al., 2001). Matching simulated and observed values in rangeland may be complicated by sampling error, which may be relatively high for individual rangeland species due to their uneven distribution, in contrast to monoculture crops. Furthermore, certain simulated crops (e.g. *Ambrosia psylostachia*) were used to represent multiple species in the simulation and thus would be expected to have less ability to match observed values.

The model's worst performance was for the year 1963, which had the fifth lowest spring precipitation on record (Apr.–June, 103 mm) followed by the fifth highest summer precipitation (July–Sept., 367 mm) for the period 1900–2015. Despite the dry early conditions, measured values of *Bouteloua gracilis* standing mass in 1963 exceeded the 10-year mean for the light and moderate grazing treatments. Apparently, *Bouteloua gracilis* was able to shift its production to later in the year when moisture was available, but the model was not flexible enough to allow such a dramatic temporal shift in production. This raises the question of how the model would perform in arid environments where production is more in sync with precipitation than temperature and time of year.

Despite its limitations, the model performed well when addressing sustainable stocking rates at Hays, Kansas. Simulated output of hay feeding, which is both an economic and production concern, and residue, which is an environmental concern, both performed according to expectations. Based on empirical levels of prior year residue remaining at the start of the next grazing season from a moderate stocking rate (Launchbaugh 1967), local experts recommend retaining ~1 Mg ha^{-1} standing residue throughout the winter. Because standing residue falls to the ground and becomes litter throughout the winter, maintaining at least 1 Mg ha^{-1} requires ~1.7 Mg ha^{-1} on Oct. 1. Our results indicated that the standing residue dropped below sustainable levels between 1 and 1.5 ha animal^{-1} (Fig. 8). This was approximately the same point at which a manager would be required to purchase supplemental feed during the summer and fall. From a manager's perspective, these concerns must be balanced against the decision to increase stocking rates.

5. Conclusions

The ability of the APEX model to simulate total aboveground biomass production for multiple plant communities at a single ecological site was demonstrated. The model's sensitivity to individual crop parameters and different precipitation scenarios indicated potential for simulating competitive species dynamics under different management and climate scenarios. It also indicated that the simulated vegetation community, which could be influenced by grazing and other management decisions, will interact with climate in determining maximum biomass production and when it is produced. Simulating biomass of individual species, rather than the sum of all species, is an area that needs improvement. The model would also benefit from testing at additional sites to identify any spatial trends in model performance. To meet the objectives of CEAP, the model should also show its ability to accurately simulate biomass production while being grazed by livestock and other herbivores. Additional modifications, not described here, have already been added to the model to better simulate grazing, but they have yet to be rigorously tested.

Acknowledgements

This material is based upon work supported by the Natural Resources Conservation Service, U.S. Department of Agriculture, Conservation Effects Assessment Project for Grazing Lands, under Cooperative Ecosystem Studies Unit agreement number 68-7482-15-513. We are grateful to Avery Meinardus, Texas A&M AgriLife Research, for providing weather and soil input files for the site.

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