

Comprehensive evaluation of the improved SPUR model (SPUR-91)

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Abstract

SPUR (Simulation of Production and Utilization of Rangelands) is a physically-based model designed to simulate the complexity of rangeland ecosystems (Wight and Skiles, 1987). Results of extensive validation testing in Texas indicated a need to modify the model to improve submodel integration and procedural guidelines. A description of the modified model (SPUR-91) is provided. A sensitivity analysis was conducted, examining the influence of changes in model output corresponding to perturbations made to individual input parameters. The model was then extensively validated using a Texas data set composed of simultaneous measurements of hydrology, plant, livestock, and meteorological parameters.

Results of validation testing of SPUR-91 confirmed that the model: (1) predicted initial soil water content within 3% of observed; (2) predicted evapotranspiration, even under very low cover conditions, within 1% of observed; (3) provided a good correlation of temporal fluctuation ($R = 0.72$) of observed herbaceous production, the observed 4-year mean live standing crop for the major individual species was predicted within 1–13%; (4) could produce a determinant-type growth curve to approximate the long-term response of shrubs and trees; and (5) responded to management (grazing, vegetation manipulation) in a manner consistent with observations. A discussion of why modifications to SPUR improved the performance of SPUR-91 is presented.

Keywords: Model evaluation; Rangeland ecosystems; SPUR

1. Introduction

Simulation of Production and Utilization of Rangelands (SPUR) is a physically-based model developed by the USDA-ARS and designed to provide biophysical simulation capability for rangeland ecosystems (Wight and Skiles, 1987). The ability of a computer model to simulate the

complexity of ecosystem function and predict ecosystem response to various management practices has great potential as a research tool and as a decision aid to resource managers. However, resource managers are reluctant to use models that cannot provide consistent, reliable results. Extensive validation is the only way to verify a model's predictive capability.

Individual submodels of SPUR were validated by the ARS teams which developed them. Results of these submodel evaluations are presented in

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Wight and Skiles (1987). But the many critical decisions that must be made by developers when integrating the various submodels into a unified working model can only be satisfactorily verified through rigorous validation of the complete model. This level of verification requires the use of extensive, long-term data sets with concurrent hydrology, plant, and animal data. A limited validation of the plant–animal interface had been conducted by Stout et al. (1990), who concluded that the model was unable to adequately predict biomass production. However, no validation of SPUR had been conducted using a data set which encompassed all three major components of the model (hydrology, plant, animal). Therefore, the effectiveness of the hydrology–plant interface had not been rigorously tested.

The model was evaluated using several extensive data sets from diverse sites in Texas. This initial evaluation revealed a number of source code programming errors and an inability of the model to simulate short-term runoff, growth responses of individual perennial species through time, shrub/tree growth dynamics, evapotranspiration and soil water content under very low cover conditions, and long-term stability of plant species composition where annuals and perennials co-occur. These problems severely limited the model's general application. The model was therefore modified to enhance flexibility of the plant growth model and to improve intercommunication between the hydrology and plant components (Carlson and Thurow, 1992).

The objectives of this paper are to: (1) describe the modified model, (2) outline the calibration and validation procedures, (3) present results of the validation and sensitivity analysis, and (4) discuss the structural and procedural changes incorporated into SPUR-91 which result in improved performance compared to SPUR.

2. Methods

2.1. Model description

Original SPUR model

SPUR is composed of five basic submodels (Fig. 1). The climate module operates indepen-

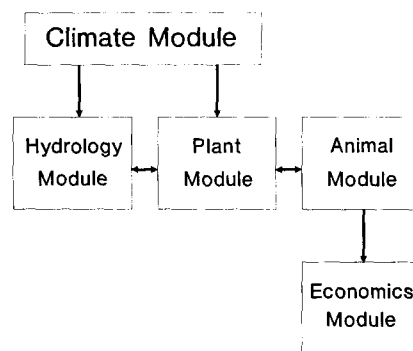


Fig. 1. Linkage of submodels within SPUR-91.

dently of the rest of the model and provides daily inputs of precipitation, maximum and minimum temperature, solar radiation, and wind run. The hydrology component maintains a daily water balance and calculates snow accumulation and snowmelt. In addition, the basin-scale version calculates streamflow and sediment transport. The plant module tracks carbon and nitrogen flows through various live and dead state variables, and has the potential to simulate competition between individual species. The animal component simulates herbage removal by both wildlife and livestock, and predicts weight gain by livestock on a steer-equivalent basis. The economics component is a simple application of cost–benefit analysis. Two versions of SPUR address different levels of landscape resolution. The field-scale version was designed to simulate plant and animal interactions on a pasture-or field-level. The basin-scale version was designed to simulate small basin watershed processes (Carlson and Thurow, 1992).

Consistent deviations between values for predicted and observed plant biomass, species composition, and hydrology output variables indicated weaknesses within the original SPUR model. Specific areas of substantial error were: (1) consistent underprediction of evapotranspiration and overprediction of deep drainage on sites with low vegetation cover, (2) inability to predict the general timing and magnitude of individual species growth during all years simulated, and (3) instability in long-term plant species composition.

This analysis revealed that hydrology input parameters had little influence over plant outputs, and vice versa. The consistent patterns of inaccuracy between observed and predicted outputs, in conjunction with results from the original sensitivity analysis, demonstrated a need for some model revision. The major problems addressed in this revision process are discussed below.

Structural modifications to SPUR

As with any model, SPUR contains a variety of limitations or shortcomings which are primarily dependent on simplifying assumptions adopted in the conceptual development phase. These assumptions are discussed in the documentation chapters of individual submodels in the user guide and documentation provided (Wight and Skiles, 1987). Other limitations or shortcomings were due, in part, to integration decisions which were apparently based on limited information. The evaluation process of SPUR conducted at Texas A&M University verified the initial conclusions of ARS modelers: the link between the hydrology and plant submodels was inadequate (MacNeil et

al., 1987). Modification efforts were therefore directed primarily at improving hydrology–plant intercommunication. Problems addressed in the modification procedure (Fig. 2) included inappropriate design and integration, mechanistic or functional inadequacies, and logic errors. Major structural changes included:

1. soil moisture conditions initialized by soil layer rather than for the soil profile as a whole;
2. subroutine alteration to permit more than one soil layer below the root zone in the field-scale model (plant-available water and deep drainage redefined accordingly);
3. change in the timing of the onset of senescent shoot death;
4. incorporation of option to over-ride subroutine that reduced late-season photosynthesis according to age;
5. correction of coding errors for “critical” plant parameters (on–off switches);
6. addition of new plant parameter to partition rooting depth of individual species;
7. creation of new controlling variable (mean soil water potential rather than soil water potential of wettest layer) for root mortality and shoot

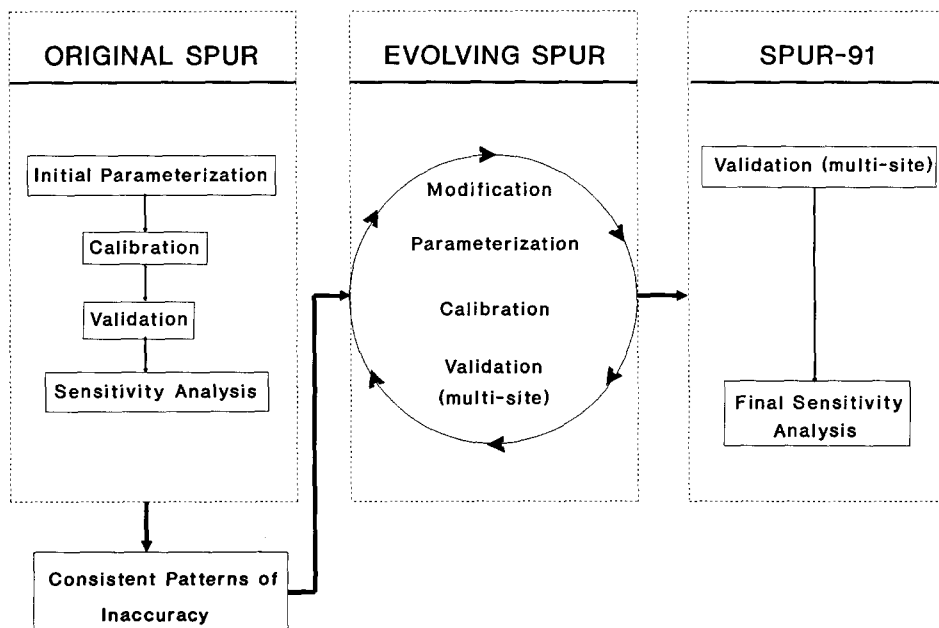


Fig. 2. The process used to evaluate and modify the SPUR model.

death, and for photosynthesis based on individual species rooting pattern;

8. soil evaporation parameter and evaporation depth tied to amount of standing cover, supplied by the plant component;
9. upland sediment production algorithms added to the field-scale version.

Additional changes are outlined in Carlson and Thurow (1992).

Procedural modifications to SPUR

Original SPUR documentation provided little guidance as to the ramifications of input parameter value selection decisions. In particular, 23 of the 51 plant input parameters are dimensionless scalars or coefficients with little meaning outside the model. The user guide (Wight and Skiles, 1987) provided little explanation of how these scalars were used within the model and where and how they affected various plant processes and, in particular, model outputs. An updated and expanded user guide was developed for the modified model (Carlson and Thurow, 1992). This new user guide includes more detail about actual model function and how changes in different parameters may affect various outputs and why. It also provides diagnostic and trouble-shooting sections based on previous users' experience, and indicates how to handle "special case" problems such as simulating shrubs and annuals given model limitations.

2.2. Data collection

Data used for the sensitivity analysis and validation were collected 22 km north of Throckmorton, TX (33°20'N, 99°14'W). Climate is semi-arid continental with approximately 650 mm average annual precipitation which is distributed bimodally. Soils were silty clay loams located on upland slopes (1–3%). The herbaceous component was a mixture of warm-season midgrasses and shortgrasses and cool-season midgrasses and forbs (Heitschmidt and Dowhower, 1991). The dominant shrub was honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) which provided about 30% cover.

Non-weighable lysimeters (area = 25 m²) were used to monitor various hydrologic processes and vegetation characteristics from 1986 to 1989 (Carlson et al., 1990). Data were collected from three replicates of three cover types: bareground (BG), herbaceous vegetation only (H), and herbaceous vegetation with a mesquite overstory (one single-stemmed tree per lysimeter) (H + M). When the lysimeters were installed, detailed soil profile descriptions and soil analyses were conducted (soil texture, bulk density, desorption, hydraulic conductivity, soil organic matter and soil aggregate stability). Volumetric soil water content was monitored at 10 depths on a weekly basis using a site-calibrated neutron probe. Deep percolation was calculated on a monthly basis by determining the net inputs of water reaching 305 mm. Runoff and sediment were collected following each storm event. Evapotranspiration was calculated weekly using the water balance equation:

$$ET = P - R - D \pm S$$

where ET = evapotranspiration including interception losses, P = total precipitation, R = runoff, D = deep percolation, and S = change in soil water storage. A micrologger weather station on site recorded ambient atmospheric conditions, including maximum, minimum, and average daily temperature, precipitation, storm duration and intensity (5-min intervals), solar radiation, humidity and wind run.

Herbaceous standing crop was characterized (live lamina, dead lamina, LAI by species, and litter cover) each month from March through November. Similar areas outside lysimeters were used to establish the relationship between LAI and standing biomass (Heitschmidt and Dowhower, 1991). Vegetation was clipped in February of each year to simulate a high-intensity, short-duration grazing regime. The seasonal trends in leaf area of mesquite were estimated using image analysis (Ansley et al., 1992). Data were used from livestock weight gain studies on nearby pastures (Heitschmidt et al., 1982a,b).

2.3. Sensitivity analysis

A sensitivity analysis was conducted for SPUR-91 by increasing and decreasing one input

parameter at a time by 20% from its base value and comparing the 10-year mean of each output variable with a base-run 10-year mean. A value of 20% was selected as the reasonable range of variance for selection of input parameter values by model users. For some input parameters, a range different than 20% was chosen to better represent the expected or likely range of values. The annual output variables selected for comparison were runoff, evapotranspiration, deep drainage, plant-available water, and sediment production. In addition, the following plant component state variables, averaged over 24 dates per year, were selected for comparison: standing live phytomass, live root phytomass, standing dead phytomass, dead roots, litter, organic matter, and soil inorganic nitrogen. This was done for all three cover types (bare ground, herbaceous vegetation only, and herbaceous vegetation with a mesquite overstory).

2.4. Parameterization, calibration and validation procedure

Actual field data and suggestions taken from *SPUR-91: User Guide and Workbook* (Carlson and Thurow, 1992) were used to initialize the approximately 130 input parameters required by the field-scale version of the model for each lysimeter. The hydrology and animal components are comprised primarily of physically-based parameters, therefore model parameterization decisions used actual data. These values were not changed during calibration. Plant input parameters were assigned values based on field data (for state variables), suggestions from the new user guide, and pertinent literature. Because snow is a minor component of the system, this subroutine had no impact on the validation. Simulation runs were calibrated for 1986. During calibration, the plant parameters found to be most sensitive were adjusted to varying degrees (10% to 20%) in an attempt to improve simulation results.

Validation results were analyzed using SAS (1988) REG and CORR procedures. Correlations and regressions were run to compare results of SPUR-91 with actual data for a variety of outputs. Validation results described as “adequate”

met the Dent and Blackie (1979) requirements for predictive capability (slope not different from one, intercept not different from zero). One lysimeter from each cover type was selected for presentation based on final validation results. Lysimeters selected were neither the best nor worst case; however, there was very little difference (less than 5%) in the results between lysimeters of the same cover type. An indication of model accuracy using standard deviations around observed data means is not included because the primary interest of this effort was to focus on consistent patterns of inaccuracy which might indicate model weakness or inflexibility.

3. Results and discussion

3.1. Sensitivity analysis

Ongoing evaluation and refinement of simulation models is a necessary activity which enables modeling tools to improve by evolving to respond to user experience as well as new information. A critical part of this evaluation process is a detailed sensitivity analysis which provides valuable information on how the magnitude of output response is associated with variation of single input parameters, and can provide some superficial indication as to how the parameters interrelate (Carlson et al., 1993). MacNeil et al. (1987) concluded from their sensitivity analysis of SPUR that the plant and hydrology components seemed “too independent”.

The SPUR-91 sensitivity analysis showed a greater response of plant output variables to changes in hydrology input variables, and vice versa. The curve number was the parameter which most influenced the various hydrology output variables. The phytomass-to-leaf area conversion factor, theoretical maximum net photosynthetic rate, maximum temperature for positive plant activity, species-specific rooting depth, julian day that senescence begins, and additional shoot death after senescence were among the ten most important parameters influencing hydrology output variables. The resultant change from the base value, however, was generally less than 20%.

There were only a few hydrology parameters that significantly influenced plant output variables (soil evaporation parameter, curve number, and -0.3 and -15 bar volumetric water content of the soil layer). These parameters were sensitive (5 to 50% change in base value) and therefore require accurate parameterization for optimum model performance.

By comparing the results of the sensitivity analyses for different plant cover types, the user can begin to understand how parameter interactions affect model results. For example, the curve number was a very sensitive parameter in all three cover types as it affected hydrology output variables. However, the curve number was more sensitive on the herbaceous-covered sites than on the herbaceous + mesquite-covered sites in terms of effects on plant component output variables. Clearly, other variables describing plant growth processes were interacting with variables affected directly by the curve number (hydrology variables) to give this variation in sensitivity. Detailed results of the sensitivity analyses for the three different vegetation cover types are presented in Carlson and Thurow (1992).

3.2. Validation

Hydrology

The original SPUR, which initialized soil moisture condition for the soil profile as a whole,

produced deviations of -20 to 60 mm between observed and simulated soil water contents in each of seven soil layers during the first two years of simulation, resulting in a net overprediction of total soil water content by 15–30%. This procedure was unrealistic, especially for rangelands, where major differences in soil texture may occur throughout the profile and where hardpans may restrict flow between soil layers.

Also, because plant processes in SPUR were controlled in part by the soil water content (i.e. soil water potential) in upper soil layers, this inability to closely predict soil water content of individual layers caused very poor correspondence in the timing and magnitude of observed and predicted vegetation production and in plant species composition.

SPUR-91 initializes soil water content by layer, resulting in prediction of 4-year mean soil water contents within 8% of observed values on all treatments (Table 1). The temporal fluctuation of weekly soil water contents generated by SPUR-91 were poorly correlated ($R = -0.23$) with observed SWC on the BG treatment but strongly correlated with observed SWC on the H ($R = 0.91$) and H + M ($R = 0.90$) lysimeters (Fig. 3).

Evaporation was consistently underestimated by about 30% during SPUR simulation runs of bare soils. Actual soil moisture data from bare soil lysimeters showed that evaporation was oc-

Table 1

Simulated and observed 4-year water balance in mm (and as a percent of precipitation received) for bareground, herbaceous, and herbaceous + mesquite cover types for three replicates of each treatment

	Observed		SPUR-91	
Precipitation	2682		2658	
<i>Bareground</i>				
Runoff	665a	(24.8)	467b	(17.6)
Evapotranspiration	2057a	(76.7)	2066a	(77.7)
Deep percolation	36a	(1.3)	112b	(4.5)
<i>Herbaceous</i>				
Runoff	44a	(1.6)	101b	(3.8)
Evapotranspiration	2710a	(101.0)	2539b	(95.5)
Deep percolation	27a	(1.0)	21a	(0.8)
<i>Herbaceous + mesquite</i>				
Runoff	182a	(6.8)	168b	(6.3)
Evapotranspiration	2550a	(95.1)	2544a	(95.7)
Deep percolation	17a	(0.6)	0b	(0.0)

Means in a row followed by the same letter are not significantly different ($P > 0.05$).

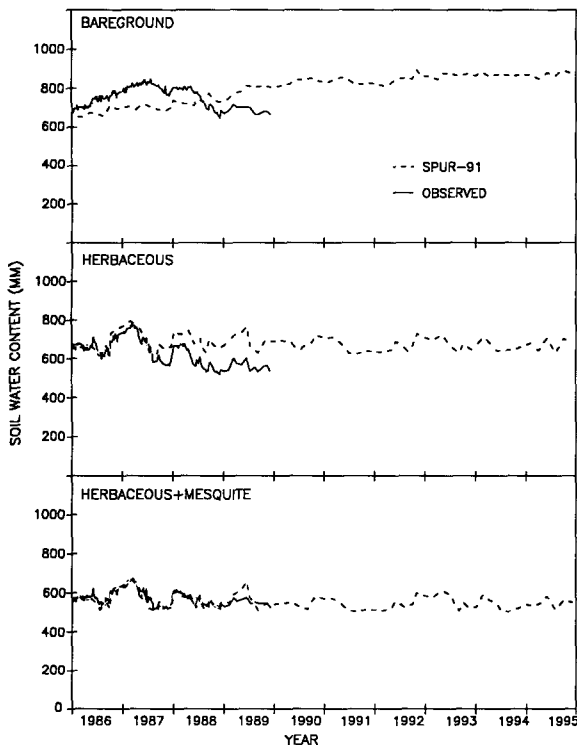


Fig. 3. Simulated and observed weekly total water content (mm) in bareground (BG), herbaceous (H), and herbaceous plus mesquite (H+M) lysimeters from 1986–1989 and predicted weekly water content from 1990–1995.

curing from soils as deep as 300 mm. The depth to which evaporation can occur in the SPUR model was pre-set to 76 mm. In addition, Ritchie's evapotranspiration model used in SPUR (Ritchie, 1972) tends to underpredict evaporation losses under bare soil conditions because wind speed and vapor pressure deficit are not included in the equations to obtain potential evaporation.

In SPUR-91, the soil evaporation parameter and depth of soil evaporation (76 to 157 mm) are linked to amount of vegetation cover, supplied on a daily basis by the plant component. This change improved evapotranspiration predictions under low or no cover conditions, while permitting the original evapotranspiration model design to remain unchanged under conditions of greater vegetative cover. SPUR-91 predicted observed 4-year total evapotranspiration (ET) within 6% on all treatments (Table 1). The correspondence of

temporal fluctuation between observed and predicted monthly ET on the BG site ($R = 0.62$) and both vegetated sites ($R = 0.82$) was adequate (Fig. 4).

Predicted monthly runoff did not adequately reflect observed monthly runoff ($R = 0.37$ to 0.58) for any cover type, an inherent problem of the curve number technique (USDA-SCS, 1972) used. However, SPUR-91 closely predicted the proportion of runoff in the total water budget for all cover types (Table 1). Deep percolation was a small component of the water budget on all three cover types. The model accurately predicted that deep percolation accounted for less than 1% of precipitation received on the H and H + M cover types (Table 1).

Plant

The plant component of SPUR could not simulate multiple growing seasons. The original de-

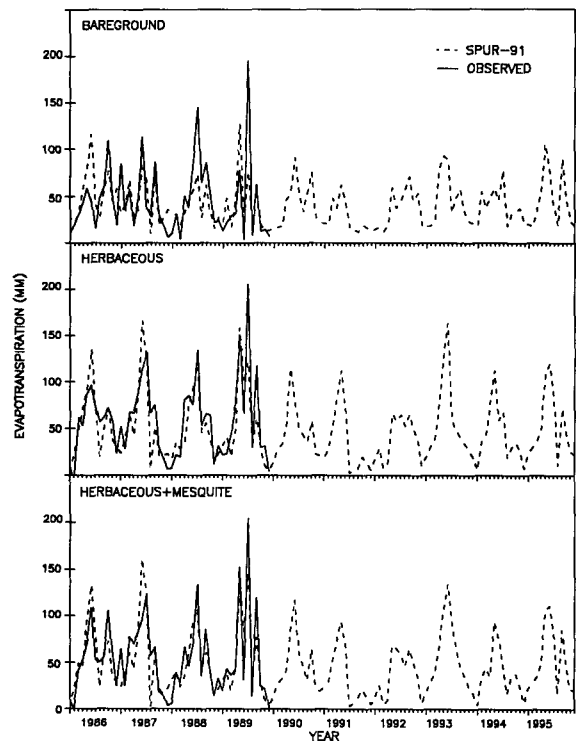


Fig. 4. Simulated and observed monthly evapotranspiration from bareground (BG), herbaceous (H), and herbaceous plus mesquite (H+M) lysimeters from 1986–1989 and predicted monthly evapotranspiration from 1990–1995.

sign reduced photosynthesis as the season progressed according to leaf age. Hanson et al. (1987) documented this reduction as a way to mimic late-season regrowth. However, this assumes that no new leaves are produced and that increased biomass is due primarily to the extension of old leaves. This is not necessarily the case for plants growing in warmer climates with readily available soil moisture (Norman, 1991). On arid and semi-arid rangelands in warmer climates, soil moisture has more influence than temperature in controlling above-ground plant production and timing of senescence (Sims et al., 1978; Larcher, 1980). Therefore, timing of senescent shoot death was modified, giving better control of shoot death occurring mid-year due to soil moisture constraints.

Temperature, and nutrient and water availability, are more decisive factors in determining plant senescence than is leaf age (Larcher, 1980). For this reason, the option of over-riding the subroutine that reduces late-season photosynthesis according to leaf age was added to SPUR-91 so that fall regrowth could be adequately simulated on warmer sites. These changes provided accurate rates of plant dieback during seasonal dry periods, and generation of multi-modal growth curves (Fig. 2).

The 4-year mean total live standing crop was predicted within 12% by SPUR-91, but the program underpredicted the 4-year mean total dead standing crop by approximately 20–25%. The correlation of temporal fluctuation between observed and predicted total live standing crop ($R = 0.72$) was adequate (Fig. 5).

The 4-year mean live standing crop of sideoats grama was predicted within 1%, and that of Texas wintergrass within 13%. Shortgrasses and annual grasses together comprised 12% of the total 4-year mean live standing crop and 5% of the total mean dead standing crop. SPUR-91 closely predicted this composition as 9% and 6% of total live and dead mean standing crops, respectively.

SPUR developers pointed out concerns of poor intercommunication between the plant and hydrology submodels. This was a major shortcoming, as rangeland hydrology and plant processes are closely intertwined. There was no provision

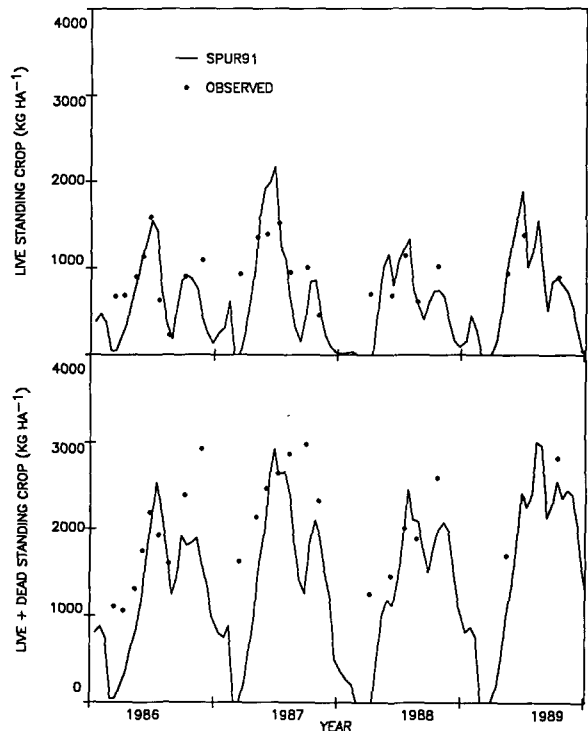


Fig. 5. Simulated and observed standing live and standing dead herbaceous vegetation (kg ha^{-1}) on herbaceous lysimeter from 1986–1989 and predicted standing live and standing dead vegetation from 1990–1995.

for “competition” between plant species for soil water. Differences in rooting patterns between species were not taken into account when calculating the effect of soil moisture on plant growth processes. Annual grass species, for example, had the same “access” to soil moisture as perennial grasses or shrubs. This problem was emphasized during initial validation runs, where annual grasses, a minor component of most of the Texas data sets, often became a dominant component after 10-year simulations and caused a decline in shrub production (a very unlikely scenario).

Photosynthesis in SPUR was controlled by the soil water potential of the wettest soil layer where roots occurred. While this method may be conceptually correct, it was impractical for use in SPUR because the hydrology component could not accurately simulate the soil water content of individual soil layers. Deviations between ob-

served and simulated soil water content for individual soil layers approached 50% or more periodically throughout simulation runs. Because of this limitation, SWAT (soil water potential of wettest layer) proved to be an insensitive control of photosynthesis. Stout et al. (1990) also experienced this problem, stating that the model was “unable to adequately predict biomass production” due in part to the interaction between soil moisture and precipitation.

A new input parameter was added which specifies to which soil layers a particular plant species’ roots has access. The mean soil water potential for each species (based on individual species’ rooting depth and parametric root distribution) controls photosynthesis in SPUR-91 rather than the wettest layer approach taken in SPUR.

These modifications provided: (1) better timing of plant growth, (2) more accurate estimates of production for individual plant species (within

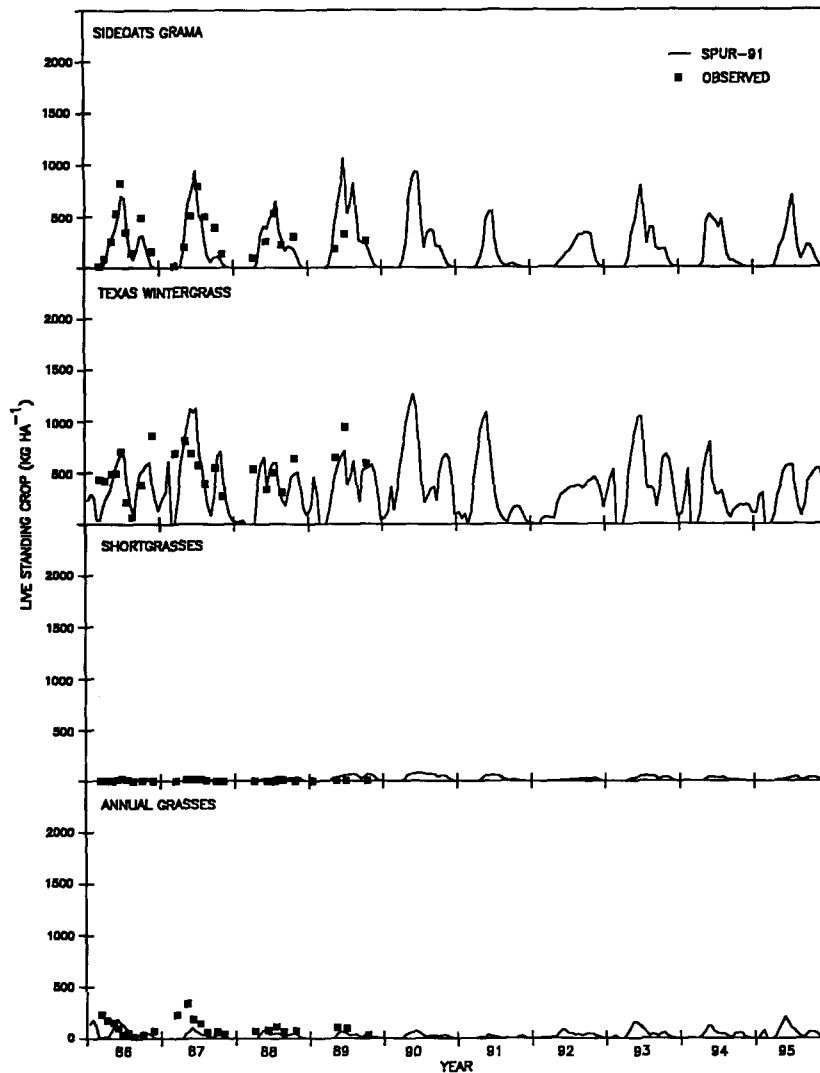


Fig. 6. Simulated and observed standing live vegetation (sideoats grama, wintergrass, shortgrasses, annual grasses) (kg ha^{-1}) on herbaceous lysimeter from 1986–1989 and predicted standing live vegetation from 1990–1995.

10% for herbaceous perennials), and (3) stability in long-term relative species composition. SPUR-91 predicted that sideoats grama and Texas wintergrass would remain relatively stable and important components of the community, while shortgrasses and annual grasses would remain a minor component of the system over a 10-year period (Fig. 6). This is in contrast to SPUR's predicted dominance of annuals and shortgrasses.

The total production of herbaceous vegetation was slightly lower when mesquite was present. A determinant-type growth pattern for mesquite could be generated using SPUR-91 by setting specific parameters outside the suggested ranges. These perturbations were made because the model does not include shrub/tree growth response algorithms pertaining to the woody component or the proper timing of the effect of environmental factors on woody growth processes. The procedure and reasoning for these perturbations are outlined in the updated user guide (Carlson and Thurow, 1992). Correlations between the observed temporal variation and predicted ($R = 0.71$) variations indicated that the model did an adequate job at estimating the general response of mesquite. A fairly consistent pattern and magnitude of growth could be maintained from year to year using the SPUR-91 model, and mesquite remained a stable component of the system over ten years (Fig. 7).

Animal

SPUR-91 predicted the 10-year mean animal weight gain for the 5-day grazing period in February as 0.11 kg day^{-1} on H + M sites and 0.23 kg day^{-1} on H sites. These estimates are less than the observed $0.45\text{--}0.68 \text{ kg day}^{-1}$ typical for the area and season for a short-duration grazing regime (Heitschmidt et al., 1982a,b). The deviation between predicted and observed weight gain may have been due in part to inaccurate simulation of the nitrogen content of forage, especially that of standing dead. The nitrogen cycling sub-model within SPUR-91 was based on limited data and has not been satisfactorily verified.

3.3. Procedural modifications

The quality of model documentation, model operation, and the model/user interface often determines the success or failure of model application. Parameterization is a major time investment for users, especially so for complex models such as SPUR. The documentation and user guide accompanying SPUR (Wight and Skiles, 1987) was not "user-friendly". The general format of individual chapters was not consistent. This disjointed presentation made it difficult to read and to determine the location of specific information desired. The documentation section for individual submodels was, for the most part, informative

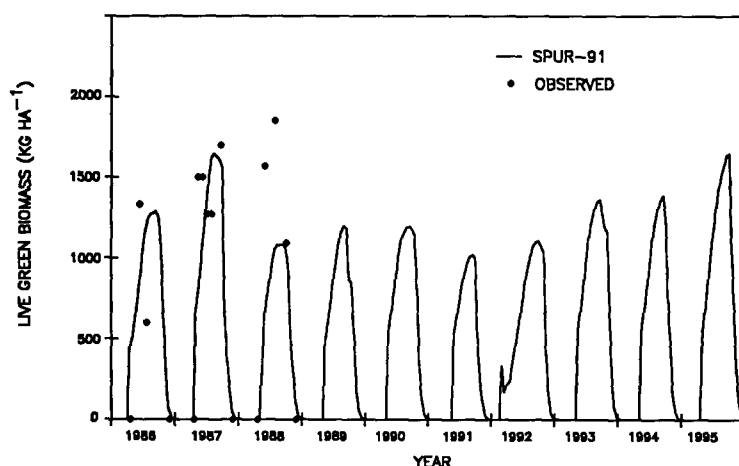


Fig. 7. Simulated and observed mesquite live green biomass (kg ha^{-1}) on herbaceous plus mesquite (H + M) lysimeters from 1986–1988 and predicted mesquite live green biomass from 1989–1995.

and complete, although model shortcomings and simplifying assumptions were often not explicitly stated. The manual lacked documentation on how the individual submodels were integrated. Some of the most important design decisions modelers must make involve interfacing of submodels, yet the documentation section provided little information into the rationale used to link submodels within SPUR. Adequate operating instructions and diagnostic information were missing. This presented problems in interpretation of model output and in source code modification.

Natural resource managers and research personnel are the primary model users, and the format and structure of the user guide needs to reflect this. A new user guide and workbook (Carlson and Thurow, 1992) was prepared with a more instructional format. Separate chapters provide: basic start-up information, parameterization guides for all input files, model operation and diagnostics, sensitivity analysis in graphic form, and a variety of appendices with more detailed information. More tables and graphs were included in the parameterization guides to help with value selection. Detailed explanations of how individual parameters affect model function and model output were included. A trouble-shooting guide and diagnostic section provides the novice user with potential solutions to common simulation problems. This includes “special case” problems, such as how to simulate growth of trees and large shrubs within the constraints set by model limitations.

Creation of input files was extremely tedious, and provided many opportunities for run-time errors. Therefore, the UTIL system, a Universal Text Integration Language developed by the USDA-ARS (1991) was added to SPUR-91. The UTIL program has markedly improved input file creation. File format is consistent from one run to the next and speed of data entry is optimized.

4. Conclusions

SPUR-91 appears to have the potential for aiding in the assessment of various management practices on rangelands. Currently, however, the

model is more reliably used to predict general trends of management responses rather than absolute values. The modifications incorporated into SPUR-91 have improved the intercommunication between the hydrology and plant components. The improvement in estimation of herbaceous biomass provided by SPUR-91 is due in part to modifications to the original model and in part to increased understanding and insight into model function provided by the updated user guide (Carlson and Thurow, 1992). The greatest impact that these two improvements had was on superior prediction of *individual* species performance. There were dramatic differences between the two models in both short-term and long-term species composition predictions.

SPUR-91 still cannot predict response of some individual species despite modifications. Species such as sideoats grama are more easily simulated because they have a regular pattern of growth. Species like wintergrass, with irregular patterns of growth, are more difficult because they are influenced by a complex interaction of controlling factors. Nor is the model designed to simulate the growth processes of non-herbaceous vegetation. There are no algorithms for light attenuation, nor any accounting for woody growth or respiration of woody tissue, etc.

The iterative process of design, implementation, and evaluation is the key to development of models which have the capability of accurately predicting the effects of natural resource management and solving problems in a consistent manner. We suggest that increased flexibility in the plant component could be made by tying the phenology of plant processes to more physically-based variables (biotic and/or abiotic). The nitrogen cycling submodels will need to be upgraded as more information becomes available through data collection and interpretation activities. The inability to more accurately predict short-term runoff is a weak link between the hydrology and plant components. A modified version of the model which replaces the curve number technique with an infiltration-based model would have the potential to strengthen the hydrology–plant interface in SPUR-91. More work needs to be done with the animal–plant interface concerning

season-and year-long animal performance and predicted animal diets compared to observed forage intake.

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