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Development and Validation of a Dynamic Model of Growth and Quality for Cool Season Grasses

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Summary

A daily time step model simulating growth and quality of cool season grasses was developed and validated for smooth brome (*Bromus inermis* Leyss.) under varying environmental and management conditions. Growth predictions are based upon genetic potential, environmental temperature, leaf area, soil moisture, and nitrogen fertilization rate. Daily potential growth rate is a composite of two functions—one relating grass species maximum growth rate to minimum, optimum, and maximum temperatures for plant growth, and another relating daily minimum and maximum air temperatures to time. Multipliers are developed for available leaf area, moisture, and nitrogen, and the minimum of these values modifies the daily potential growth rate to determine daily plant production. Change in sward dry matter digestibility (*DMD*) is a function of forage material present, daily forage growth, and environmental temperature. For dry matter (*DM*) production, the relationship between model (*Y*) and observed (*X*) estimates (kilograms of dry matter per hectare) yielded the regression equation: $Y = 218 + 0.94X$; $SE = 431$; $R^2 = 0.98$. The relationship between model (*Y*) and observed (*X*) estimates of *DMD* (%) gave the regression equation: $Y = 2.24 + 0.97X$; $SE = 1.78$; $R^2 = 0.90$. The above validation shows that the mathematical logic contained within the plant model accurately predicted smooth brome production and changes in forage quality. Intercept and slope values were similar to 0.0 and 1.0, respectively, and standard error values were similar to observed experiments.

Introduction

Plant species, temperature, soil moisture, photoperiod, fertilization rate, and management schemes influence the observed patterns of change in forage production and quality. Variation in forage production over time is partially due to environmental factors which cannot be controlled, and partially due to management factors which can be controlled. Many experiments have been conducted dealing with the effects of management on forage production; however, many of these have not been fully utilized to gain a better understanding of the interactions that control the growth process.

Much of our knowledge of plant growth is qualitative, because, in a single experiment, it is impossible to control and vary all, or even a significant number, of the factors that influence the growth process. In order to understand more fully the growth process, much of this knowledge must be identified in a quantitative context. A systems approach has been taken (Angus *et al.*, 1981) to assist in quantifying these interactions. When applying mathematical functions to biological relationships, model structure becomes important. Empirically based models, while lacking complexity, can often be applied only to specific situations. In some cases, they lack the ability to provide quantitative estimates of many interactions. On the other hand, the information required for complex models restricts their use for general applications. An intermediate approach, based upon a few physiological principles, has also been taken (Holt *et al.*, 1975; Torszell & Kornher, 1983; Porter, 1984). This approach has dealt with developing a tool whereby environment $\times$ management effects on yield can be calculated for a location for which records of environmental data are available.

The objective of this modeling effort was to increase the understanding of the interactions of the factors that influence plant growth, and to act as an aid in research planning. Also to evaluate, adapt, add to, and validate a simulation model of cool season grasses (Smith & Loewer, 1981, 1983), for yield and quality of smooth brome (*Bromus inermis* Leyss) under varying environmental and management conditions.

Materials And Methods

The plant model is a daily time step simulation program designed to predict forage production and quality, utilizing a minimum number of in-

puts related to environmental conditions and plant characteristics. Growth predictions are based upon genetic potential, environmental temperature, leaf area, soil water balance and nitrogen fertilization rate (Figure 1).

Maximum growth rate (R ; kilograms of dry matter per hectare per hour) of the simulated plant species is used in conjunction with the minimum (XM), optimum (QR), and maximum (XMM) temperatures for plant growth to develop a function relating growth rate to temperature (Figure 2). This parabolic type relationship is composed of two quadratic equations, one describing growth rate between the minimum and optimum temperatures for growth and another describing growth rate between the optimum and maximum temperatures for growth. The maximum growth rate is assumed to occur at the optimum temperature for growth. Torssell & Kornher (1983) utilized a similar function in their model of Swedish ley crop production; however, they related relative growth rate to mean daily temperature.

Figure 1. General flowchart of the plant growth model.

Figure 2. Relationship between plant growth rate and minimum (*XM*), optimum, and maximum (*XMM*) temperatures for plant growth.

Daily minimum (*MIN*) and maximum (*MAX*) air temperatures (°C) of the simulated location are utilized to construct an air temperature profile (Figure 3). This profile describes daily air temperature by two functions — one from dawn to solar noon and another from solar noon to sundown. Since irradiation is not included in the model, it may need to be modified for use in climates with excessive cloud cover.

The growth rate and air temperature relationships are combined so that growth rate may be expressed as a function of time, and a daily potential growth rate may be determined. With the separation of plant terms in the model, this growth rate represents the daily potential of the sward.

Figure 3. Air temperature profile.

Model logic works on the first limiting factor concept which historically has been proposed by Liebig and Blackman, as discussed by Gardner *et al.* (1985). This tends to ignore the interactions among factors. However, using the limiting factors concept is a good starting place to study agricultural yields (Salisbury & Ross, 1978). The factor present in the least amount (leaf area, moisture, or nitrogen) controls plant growth. This limiting factor modifies the daily potential growth rate to determine the final estimate of daily plant growth rate. This growth rate is integrated over the number of daylight hours to determine daily forage production. Daylight hours are calculated as a function of latitude and date. In the Swedish ley crop production model of Torssell & Kornher (1983), a different approach was taken. Growth rate was modified by the product of indices for leaf area, temperature, radiation, and soil water, rather than the minimum of these values.

Leaf area index (multiplier)

A multiplier scaled from 0.0 to 1.0, accounting for the effect of varying leaf area upon plant growth, is calculated as a function of forage yield (Figure 4). *QQ1* represents the quantity of forage (kilograms of dry matter per hectare) where leaf area does not limit growth. After growth begins, the leaf area index multiplier increases from 0.0 to 1.0 as simulated forage yield increases from 0.0 to *QQ1*, with the rate of increase dependent upon the value of *QQ1*. *QQ2* represents the quantity of forage (kilograms of dry matter per hectare) where leaf area begins to limit growth. This is the point where upper leaves begin to shade lower leaves, reduc-

Figure 4. Leaf area index multiplier. *QQ1* and *QQ2* represent forage biomass at which leaf area does not limit growth and limits growth due to shading, respectively. *QQ3* represents maximum possible yield accumulation in the field.

ing their photosynthetic capacity. The leaf area multiplier equals 1.0 as simulated forage yield increases from *QQ1* to *QQ2*. *QQ3* represents the greatest quantity of forage (kilograms of dry matter per hectare) that can accumulate in the field. The leaf area multiplier declines from 1.0 to 0.0 as simulated forage yield increases from *QQ2* to *QQ3*, with the rate of decline dependent upon the magnitude of difference between *QQ2* and *QQ3*. The leaf area multiplier equals 0.0 at *QQ3*. A similar shaped function is used in the winter wheat simulation model of Porter (1984) to account for variations in leaf area.

Soil water index

Daily rainfall, average daily temperature, soil water-holding capacity, initial soil moisture content, and latitude of the simulated location are utilized to calculate a 0.0 to 1.0 value index accounting for the effects of varying soil moisture on plant growth. Daily evapotranspiration is calculated and, along with daily rainfall, soil water content is determined. If rainfall increases soil water content above the water-holding capacity, water above the holding capacity is lost. Plant available water is defined as that water in the soil as a percentage of the soil water-holding capacity. Plant available water is utilized, in the relationship shown in Figure 5, to calculate a 0.0 to 1.0 value soil water index. A soil water index, also calculated as a function of plant available water, is utilized in the plant models of Fick & Onstad (1981) and Torrsell & Kornher (1983).

Figure 5. Soil water index

Figure 6. Nitrogen index.

Nitrogen index

Nitrogen fertilization rate (kilograms of nitrogen per hectare) is utilized to calculate a 0.0 to 1.0 value index accounting for the effect of varying nitrogen fertilization rate upon forage production (Figure 6). With moisture not limiting, maximum forage production of smooth brome occurs at approximately 120 kg of nitrogen per hectare, with production being reduced to approximately 20% of maximum with no supplemental nitrogen (Colville *et al.*, 1963; Washburn, 1969; George *et al.*, 1973). The yield with no nitrogen addition would vary with the natural nitrogen status of the soil.

Forage quality

Forage dry matter digestibility (DMD) is calculated as a function of forage material present, growth of new forage material, and environmental temperature (Equation (1)):

$$\begin{aligned}
 DMD(J) = & (SUMY(J-1) * (DMD(J-1) - (DMDRED * \\
 & \frac{(DMD(J-1) - DMDLOW) *}{(DMDNEW - DMDLOW)} \\
 & \frac{(MAX(J))}{(XM)}) + (ACTLEV(J) * DMDNEW))) \quad (1)
 \end{aligned}$$

Where: $DMD(J)$ = dry matter digestibility on day J (%); $SUMY(J-1)$ = forage accumulation on day $J-1$ (kilograms of dry matter per hectare); $DMD(J-1)$ = dry matter digestibility on day $J-1$ (%); $DMDRED$ = reduction in dry matter digestibility of the plant species (%); $DMDLOW$ = lowest dry matter digestibility of the plant species (%); $DMDNEW$ = dry matter digestibility of newly grown forage (%); $MAX(J)$ = maximum air temperature on day J ($^{\circ}C$); XM = minimum temperature for plant growth ($^{\circ}C$); $ACTLEV$ = forage production on day J (kilograms of dry matter per hectare); $SUMY(J)$ = total forage accumulation on day J (kilograms of dry matter per hectare).

This results in a negative exponential relationship between forage DMD and time, that asymptotically approaches $DMDLOW$, with the rate of decline dependent upon $DMDRED$, quantity of forage present, daily forage growth, and environmental temperature. As environmental temperature increases, forage DMD declines at a faster rate (Van Soest *et al.*, 1978).

User inputs

Inputs related to environmental conditions and plant characteristics are required to simulate forage production and quality under varying moisture conditions, nitrogen fertilization rates, and growing season lengths. Environmental inputs include: daily minimum (MIN) and maximum (MAX) air temperatures ($^{\circ}C$), daily rainfall (cm), and latitude for the simulated location.

Plant-related inputs include three temperatures for plant growth ($^{\circ}C$): (a) XM —minimum temperature for growth, (b) QR —optimum temperature for growth and (c) XMM —maximum temperature for growth. Maximum growth rate (R ; kilograms of dry matter per hectare per hour) of the simulated plant species is also required. Maximum growth rate is assumed to occur at the optimum temperature for growth. Three inputs related to accumulated forage ($QQ1$, $QQ2$, and $QQ3$; kilograms of dry matter per hectare) are required to develop the leaf area multiplier.

The following inputs related to forage quality are required to simulate daily changes in forage DMD : $DMDRED$, $DMDNEW$, and $DMDLOW$. $DMDRED$ represents the reduction in forage DMD independent of plant growth. This is the daily reduction in DMD that occurs when no new growth accumulates.

Nitrogen fertilization rate, soil water-holding capacity, initial soil water content, number of days in the run, date to begin the simulation, and quantity of forage *DM* present at the start of the simulation are also required.

Results And Discussion

Model validation included a series of 69 simulation runs designed to compare model estimates of forage production and dry matter digestibility (*DMD*) with observed experimental results. Measures of model validation included model versus observed regression equation intercept and slope values similar to 0.0 and 1.0, respectively, similar standard error (SE) values to observed experiments, large R^2 and similar means and standard deviations between model and observed estimates. Model estimates were also partitioned into the relative percentages of those occurring within 200, 400, 600, 800, and 1000 kg of dry matter per hectare of observed values for yield and 1, 2, 3, 4, and 5 units for *DMD*.

Seventeen parameters were required to calibrate the model in terms of describing the growth rate relationship, leaf area, soil water, and nitrogen indices for a given plant species $\times$ environmental combination. Once these values were determined for smooth brome, they were held constant throughout model validation. Data used for calibrating the model were not used for validation.

Input values developed for the prediction of smooth brome growth and quality are presented in Table 1. Baker & Jung (1968b) indicated that a temperature of 2.0°C was detrimental to smooth brome growth. They also found the optimum temperature for growth to be 18.3 °C, and stated that day temperature had a greater influence on growth than night temperature. Baker & Jung (1968a) noted a significant decline in smooth brome growth as day temperature increased from 31.0 to 35.0 °C.

Because instantaneous determinations of growth rate defy measurement, few data are available on the rate of smooth brome growth under ideal conditions over short periods of time. The value of the maximum growth rate was derived by minimizing the difference between model and observed estimates of forage production from several studies where observed conditions were near optimal. Through model analysis, the maximum growth rate for smooth brome was determined to be 15.3 kg of dry matter per hectare per hour.

Table 1. Input Values for the Prediction of Growth and Quality of Smooth Brome

Model input	Value
Temperatures for growth (°C)	
Minimum	4.4
Optimum	18.3
Maximum	32.2
Maximum growth rate (R; kilograms of dry matter per hectare per hour)	15.3
<i>QQ1</i> (kilograms of dry matter per hectare)	1,350
<i>QQ2</i>	3,950
<i>QQ3</i>	11,200
<i>DMDRED</i> (%)	0.5
<i>DMDNEW</i>	80.0
<i>DMDLOW</i>	42.0

Brougham (1956) monitored regrowth and light interception of a ryegrass (*Lolium perenne*) sward following various defoliation intensities (2.5, 7.6, and 12.7 cm remaining). As defoliation intensity increased, additional time was required to intercept 95% of the available light. However, for all defoliation intensities, forage yield at 95% light interception was approximately 1,400 kg of dry matter per hectare, which is similar to the value of 1,350 kg of dry matter per hectare for *QQ1* in Table 1. In the same study, the interaction between accumulated dry matter and accumulated leaf area over time indicated that, for the 12.7 cm defoliation intensity, accumulated leaf area increased to a certain level and then declined. Forage accumulation at the peak leaf area equaled 4,210 kg of dry matter per hectare, which is similar to the value of 3,950 kg of dry matter per hectare for *QQ2*.

Richards *et al.* (1962) monitored changes in total digestible nutrient (*TDN*) content of smooth brome over time. The regression of *TDN* content (*Y*) on days after April 10 (*X*) yielded the equation: $Y = 77.0 - 0.3X$. Colburn *et al.* (1968) calculated a regression equation of $Y = 74.0 - 0.4X$ between *DMD*(*Y*) and days after May 11 (*X*) for orchardgrass (*Dactylis glomerata* L.). Mellin *et al.* (1962) sampled timothy (*Phleum pratense* L.) at weekly intervals from May 27 until August 5, and calculated a regression equation of $Y = 84.9 - 0.48X$ between *DMD*(*Y*) and days after May 27 (*X*). The value of 80.0%, for *DMDNEW* presented in Table 1 for

Figure 7. Effect of nitrogen fertilization rate on observed and model estimates of smooth brome yield. (Source: Engel, 1983).

smooth brome is consistent with the Y -intercept values of the above equations. The value of 0.5 for *DMDRED* (Table 1) is greater than the mean of the above slope values. This is expected since *DMDRED* represents the daily reduction in *DMD* that occurs when no new growth accumulates. Slope values presented above include the effect of new forage growth on changes in forage *DMD*.

Data presented in Figure 7 come from a trial designed specifically for validation of the plant model. These data allow observation of patterns of forage accumulation over time under varying nitrogen fertilization rates. In the observed data, an interaction existed between harvest data and nitrogen fertilization rate. For the 0.0 kg of nitrogen per hectare rate, forage yield increased linearly as harvest date was delayed. For the 84.2 kg of nitrogen per hectare rate, however, forage yield increased to a point and then declined as harvest date was delayed. This response was possibly due to a lack of soil moisture late in the growing season. The plant model accounted for this interaction by predicting forage yield for the 0.0 kg of nitrogen per hectare rate within at least 200 kg of dry matter per hectare at all sampling dates. For the 84 kg of nitrogen per hectare rate, the plant model simulated yield to within at least 200 kg of dry matter per hectare between Julian days 110 and 145. As observed yield declined after Julian day 145, the model simulated a zero growth rate due to lack of soil moisture. Presently, the plant model does not contain logic which simulates the decay of plant material. Therefore, simulated yield will not decline

Figure 8. Model and observed estimates of smooth brome production (kilograms of dry matter per hectare).

with delay in harvest date as was observed in this study. In the Swedish ley crop production model of Kornher & Torssell (1983b) a significant soil water $\times$ nitrogen fertilization rate interaction was also observed.

The relationship between all model and observed estimates of smooth brome production used in model validation is presented in Figure 8. The plant model provides an accurate estimate of smooth brome production under varying moisture conditions, nitrogen fertilization rates and growing season lengths. The regression of model (Y) versus observed (X) forage yield (kilograms of dry matter per hectare) estimates gave the equation: $Y = 218 + 0.94X$; $SE = 431$; $R^2 = 0.98$. Mean model and observed estimates were 4,350 and 4,390 kg of dry matter per hectare, respectively. Model and observed standard deviation estimates were 2,540 and 2,650 kg of dry matter per hectare, respectively. To evaluate absolute differences between observed and model estimates, differences between observed and model values were calculated. The percentages of those occurring within various ranges are given in Table 2. Ninety-two per cent of all yield predictions were within at least 800 kg of dry matter per hectare, while 97% were within at least 1,000 kg of dry matter per hectare of observed values.

Angus *et al* (1981) obtained R^2 values ranging from 0.67 to 0.92 between model and observed forage production estimates of timothy produced in Sweden. They noted an effect due to latitude and stated that

Table 2. Frequency of Differences Between Observed and Model Estimates of Forage Production and Quality

Item	Percentage of estimates within indicated difference
Forage production	
(kilograms of dry matter per hectare)	
0–200	44
201–400	73
401–600	83
601–800	92
801–1,000	97
Dry matter digestibility (%)	
0.0–1.0	30
1.1–2.0	65
2.1–3.0	70
3.1–4.0	85

their model underestimated forage production north of latitude 59 N due to greater assimilate storage and subsequent mobilization in northern regions due to more severe winters.

Torssell & Kornher (1983) calculated an R^2 value of 0.96 between model and observed estimates of forage production in their model of Swedish ley crops. In the alfalfa model of Fick & Onstad (1981) the regression between observed (Y) and model (X) forage yield (kilograms of dry matter per hectare) gave the prediction equation: $Y = 844 + 0.726X$; $SE = 870$; $R^2 = 0.62$. Arranging the data from our study in this format yielded the equation: $Y = -38 + 1.03X$. Kornher & Torssell (1983a) defined per cent absolute mean difference as the mean of all deviations between the absolute value of model and observed yields, as a percentage of the observed mean yield. Values for this term ranged from 15 to 20 % for the spring growth of various grass species. A value of 7.5 % was calculated from the data in our study.

The relationship between all model (Y) and observed (X) estimates of *DMD* used in model validation is presented in Figure 9. The regression of these data yielded the equation: $Y = 2.2 + 0.97X$; $SE = 1.78$; $R^2 = 0.90$. Mean model and observed estimates of *DMD* were 56.6% and 56.3%, re-

Figure 9. Model and observed estimates of smooth brome dry matter digestibility (%).

spectively. Model and observed standard deviation estimates were 8.2% and 7.7%, respectively. The absolute differences between model and observed estimates of *DMD* occurring within various ranges are presented in Table 2. Eighty-five per cent of all model estimates were within 4.0 units of observed values. Fick & Onstad (1981) calculated a regression equation of $Y = 20.10 + 0.744X$; $SE = 4.5$; $R^2 = 0.25$ between observed (Y) and model (X) estimates of *DMD* for alfalfa (*Medicago sativa* L.). They concluded that an empirical, time-based simulation of alfalfa *DMD* is not adequate. Arranging data from our study in this format gave the regression equation: $Y = 8.71 + 0.841X$.

The validation presented has shown that it is possible to predict accurately smooth brome production and quality through the use of three main groups of parameters: a plant term, an environmental term, and a management term. Driving variables in the plant term include genetic potential of the plant species and leaf area. The environmental term contains information about temperature, soil water, and day length, while nitrogen fertilization rate and harvest date drive the management term. Since the model does not account for radiation, there may be problems using it in areas with extended periods of low radiation due to cloud cover. However, the model apparently functions well in the areas where smooth brome is grown.

This modeling effort has dealt with making quantitative estimates of the interactions that influence forage production and quality. Describing factors that influence forage production such as the growth rate, leaf area, soil water, and nitrogen relationships offers new possibilities of quanti-

fying plant characteristics. This opens the possibility for a more dynamic approach to field research whereby a range of interacting variables can be measured and evaluated.

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