MODELING GROWTH AND COMPETITION OF A MULTI−SPECIES PASTURE SYSTEM

T. Zhai, R. H. Mohtar, H. D. Karsten, M. Carlassare

ABSTRACT. *Pastures are often a mixture of different plant species. The growth patterns of these mixtures are determined by the interactions and competition among the coexisting species, as well as their response and interactions with the environment. Grassland management for economic and environmental sustainability should be based on the integrated view of the pasture system and the understanding of the processes involved. Computer models are ideal to study such complex systems. Most modeling efforts have focused on binary combinations of an agronomic crop and a major weed species in agricultural systems. In this research, the GRAzing SImulation Model (GRASIM) was extended to account for growth and interspecies competition among a mixture of plant species, including grasses, legumes, and weeds. In the multispecies GRASIM, a user−specified number of species grow separately on a daily time step, competing for light, soil water, and nitrogen. Forage experiments were conducted on a naturalized pasture at the Pennsylvania State University Beef Research Farm (University Park, Pa.). The pasture was divided and rotationally stocked at two intensities (high and low). Forage biomass data from 1998 and 1999 were used to develop and evaluate the multispecies GRASIM model. The multispecies GRASIM reasonably simulated the growth dynamics of multiple species on two grazing treatments across two seasons, despite the high variability of the pasture. The model−simulated and observed biomass data for the dominant species across the two treatments and the two growing seasons gave regression coefficients of determination (R^2) ranging from 0.25 to 0.98. Model limitations and directions for future efforts are outlined and discussed. The multispecies GRASIM can be used to help evaluate coexisting species interaction and their response to the environment and provide insight into the complex mixed−species pasture ecosystem.*

Keywords. *Crop competition modeling, GRASIM, Naturalized pasture, Multiple forage species.*

Interspecies competition for light, water, and nutrients is one of the key factors determining the performance of pasture ecosystems. Because of its important role in a wide range of ecosystems, competition between plants has been studied from different perspectives. Interspecies competition is dynamic by nature, and can be understood only as it evolves over time in response to initial growth and site conditions, weather condition, and the interactions between soil and plants in the system (Graf et al., 1990a, 1990b). Computer models can be applied to cover temporal and spatial scales that are too expensive in cost and time to be studied by experimentation. Thus, modeling interspecies competition is a natural application of dynamic simulation models.

Over the past 20 years, there have been many attempts to model interspecies competition for a number of important crop/crop, tree/crop, and weed/crop systems. These models are collectively called “intercrop” models. They can be valuable in providing better insight into the intricate physiological mechanisms of plant competition. Ecologists use them to study succession patterns of vegetation, the diversity and stability of plant communities, and to help define management strategies for semi−natural ecosystems (Grace and Tilman, 1990; Grime, 1979; Harper, 1977). Plant breeders and agronomists use intercrop models to evaluate the role of specific traits (such as those related to canopy dimension and growth rates) in shaping the interaction between crop, management, and environment (WARDA, 2000).

Historically, most intercrop models are concerned with agronomic crop production systems, with an aim at simulating the competition effects of weeds or “unwanted” plants on one major cash crop and developing predictive tools for yield loss assessment (Kropff, 1988, 1993; Kropff et al., 1992; Kropff and Spitters, 1992; Kiniry et al., 1992; Wilkerson et al., 1990). These intercrop models have made significant improvement from earlier modeling efforts where simple regression of yield loss to initial plant density was used. These new generation mechanistic models take into account climatic conditions and dynamic competition among species over time, which makes them more capable of explaining the outcome of competition. However, these modeled agricultural systems typically received moderate to high resource input, and the species distributions are much more homogeneous than those in natural ecosystems. Very few models have been developed for simulating natural ecosystems such as grassland and pasture systems, which are characterized by low nutrient environments and high diversity in terms of spatial and temporal species composition. Most existing pasture models (Parsch and Loewer, 1995; Thornley, 1998; Herrero et al., 2000a,

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2000b; Mohtar et al., 1997a, 1997b) were designed for pasture with single species and thus are limited in their ability to simulate forage growth for natural pastures where many species coexist.

The goal of this research was to develop an eco−physiological model to simulate plant growth and competition for multiple plant species growing simultaneously. It is assumed that competition among plant species results in the reduction of growth due to the consumption, hence depletion, of water, nutrients, and light by other coexisting species. Specifically, the objectives of this research are: (1) to develop a multispecies model using the monospecies pasture model, GRAzing SImulation Model (GRASIM) (Mohtar et al., 1997a), and (2) to evaluate the multispecies GRASIM using data from field experiments. The new model will take into account plant competition for light, soil water, and nitrogen by partitioning these resources according to species composition in the pasture and by a growth reduction mechanism.

METHODOLOGY

THE GRASIM MODEL

GRASIM was designed to simulate pasture growth under intensive rotational grazing management where grazing is a primary forage source during the grass growing season. It accounts for carbon, nitrogen, and water cycling and their dynamic interaction in a pasture system. Detailed model structure and algorithms were previously described by Mohtar et al. (1997a, 2000). GRASIM was originally designed to simulate the growth of monoculture pasture, and its plant growth model was parameterized and evaluated using field data from an orchardgrass pasture (Mohtar et al., 1997b). In this research, modifications to GRASIM's three major components, i.e., plant growth, soil water, and soil nitrogen modules, were conducted to simulate the mixed pasture. A newly developed legume module (Chen, 2000) was used to simulate legume growth and biological nitrogen fixation.

SIMULATION OF PLANT COMPETITION

Competition for Light

Competition for solar radiation is one of the most important components of the interference between species in mixed plant communities (Goudriaan and Monteith, 1990). The GRASIM plant growth module is based on the plant leaf and canopy photosynthetic characteristics (Mohtar et al., 1997a). Its estimate of light attenuation inside the plant canopy is described by Beer's law (Monsi and Saeki, 1953) while taking the transmitted component into account.

For monoculture pasture, irradiance incident on the leaf surface within the crop canopy is:

$$I(l)=\frac{k}{1-m} I_0 \exp(-kl) \tag{1}$$

where k is the canopy light extinction coefficient, m is the leaf light transmission coefficient, l is leaf area index (LAI, m^2 leaf area/ m^2 ground area), and I_0 is the daily total irradiance above the top of plant canopy (W−min/m^2). For the simulation of light partitioning between competing species, the most common approach has been to calculate the interception of light by each species in a mixture as a function of leaf area distribution of component species (Spitters and Aerts, 1983; Graf et al., 1990b; Kropff and Spitters, 1992). Based on the analysis of Thornley and Johnson (1990), the irradiance incident on the leaves of the ith species, $I_i(l)$, in a mixture is calculated as:

$$I_i(l)=\frac{k_i}{1-m_i} I_0 \exp(-k_e l) \tag{2}$$

where

$$k_e = \frac{\sum_{i=1}^{n} k_i l_i}{l}$$

$$l = \sum l_i$$

and k_i, m_i, and l_i are the light extinction coefficient, light transmission coefficient, and LAI for the ith species in the mixture, respectively; l is the total LAI calculated as the sum of LAIs of all species; k_e is the effective light extinction coefficient calculated as the weighted average light extinction coefficient using the LAI of each species and total LAI; I_0 is the daily total irradiance above the top of plant canopy; and n is the total number of species.

GRASIM's plant growth module is driven by the solar radiation intercepted and absorbed by the crop canopy. The multispecies GRASIM simulates photosynthesis and growth of each species according to its share of photosynthetically active radiation (PAR) in the total PAR absorbed by all species in a mixture. Single−leaf instantaneous photosynthetic rate for the ith species in a mixture, P_i in $\left(\frac{\text{kg CO}_2}{\text{m}^2 \text{ leaf area}}\right)\text{sec}^{-1}$, is calculated using a rectangular hyperbolic equation of the form:

$$P_i = \frac{\alpha_i I_i(l) P_{mi}}{\alpha_i I_i(l) + P_{mi}} \tag{3}$$

where α_i is the photochemical efficiency of the ith species; $I_i(l)$ is the irradiance incident on the canopy of species i with LAI of l calculated using equation 2; and P_{mi} is the maximum photosynthetic rate of the ith species, which is calculated as a function of daily average temperature (T) as:

$$P_{mi} = P_{0i} + P_{1i}\, T \tag{4}$$

where P_{0i} and P_{1i} are light−saturated leaf photosynthetic rate parameters. Daily canopy photosynthetic rate for the ith species in a mixture is calculated by integrating equation 3 over total leaf area (L_i) of the ith species in a mixture and over daily photoperiod (h) in seconds:

$$P_{di} = \int_0^{L_i} \int_0^{h} P_i \, dl_i \, d\tau \tag{5}$$

Combining the analytical integration of equation 5 derived by Johnson et al. (1983) and the analysis of canopy photosynthesis by Thornley and Johnson (1990), the daily photosynthetic rate of species i in a mixture, P_{di} in $\left(\frac{\text{kg CO}_2}{\text{m}^2 \text{ leaf}}\right)\text{d}^{-1}$, is calculated as shown in equation 6.

$$P_{di} = \frac{k_i L_i P_{mi} h}{k_e L} \ln \left(\frac{(1-m_i)P_{mi} + \frac{\alpha_i k_i I_0}{h} \left[(1-m_i)^2 P_{mi}^{\ 2} + \frac{2\alpha_i k_i I_0}{h} (1-m_i) P_{mi} \right]^{1/2}}{(1-m_i)P_{mi} + \frac{\alpha_i k_i I_0}{h} e^{-k_e L} \left[(1-m_i)^2 P_{mi}^{\ 2} + \frac{2\alpha_i k_i I_0}{h} (1-m_i) P_{mi} e^{-k_e L} \right]^{1/2}} \right) \tag{6}$$

The potential daily plant growth for the *i*th species in a mixture is calculated by multiplying equation 6 by a conversion factor to derive the daily carbon gain (Mohtar et al., 1997a). The LAI for each species is calculated daily as a function of its daily growth (eq. 6), specific leaf area, and a linear senescence rate, as well as environmental conditions (Mohtar et al., 1997a). The current model does not explicitly simulate plant phenology.

Competition for Water

GRASIM implements a straightforward moisture balance for a free draining soil profile. It accounts for runoff from daily precipitation, water loss from evapotranspiration (ET), and leaching below the rooting zone.

As in many other models such as GLEAMS, Opus, and PRZM−2 (Ma et al., 1999), GRASIM's ET routine is energy based. It adopted Ritchie's (1972) ET model to calculate soil evaporation and plant transpiration separately. Soil evaporation is calculated in two stages based on soil moisture content. Potential plant transpiration is considered as proportional to the LAI of a plant species up to an LAI of 3. When the LAI is greater than 3, potential transpiration equals the difference between the potential ET and soil evaporation.

In the multispecies GRASIM model, potential plant transpiration for each species is calculated separately based on the solar radiation absorbed by that species in a mixture. Total potential plant transpiration is calculated daily by summing potential transpiration from all species. The calculations are outlined in the following set of equations:

$$E_{p_i} = f\left(J_{a,i}, l_i\right)$$

$$J_{a,i} = I_0 \frac{k_i l_i}{k_e l} \left[1 - \exp\left(-k_e l\right)\right]$$

$$l_i = sla_i \cdot DW_{Si}$$

$$E_{p_{Total}} = \sum E_{p_i} \tag{7}$$

where E_{pi} is the potential plant transpiration of species i (Ritchie, 1972), which is a function of absorbed solar radiation by the ith species in a mixture ($J_{a,i}$) and its LAI (l_i); I_0 is the daily total irradiance above the top of plant canopy; sla_i is the specific leaf area (m^2 leaf area (kg C)$^{-1}$) of the ith species in the mixture; DW_{Si} is the structural dry weight of species i; and E_{pTotal} is the daily total potential plant transpiration.

When soil moisture content is limiting, the plant transpiration reduction mechanisms used in the model INTERCOM for C$_3$ crop species (Kropff, 1993) are adopted to simulate the effect of water shortage on transpiration. The ratio between actual (T_a) and potential (T_p) transpiration decreases linearly with soil moisture availability when the actual soil moisture content (θ_a) falls below a certain critical level (θ_{cr}) (Doorenbos and Kassam, 1979) (eq. 8):

$$\frac{T_a}{T_p} = \frac{\left(\theta_a - \theta_{wp}\right)}{\left(\theta_{cr} - \theta_{wp}\right)} \qquad \theta_{cr} \geq \theta_a \geq \theta_{wp}$$

$$\frac{T_a}{T_p} = 1 \qquad \theta_a > \theta_{cr}$$

$$\theta_{cr} = \theta_{wp} + (1-p)\left(\theta_{fc} - \theta_{wp}\right) \tag{8}$$

where θ is the soil moisture content (mm), with subscripts denoting the critical value (*cr*), the value at wilting point (*wp*), and field capacity (*fc*). The soil moisture depletion factor (*p*) depends on plant species and evaporative demand (i.e., potential transpiration). Based on the relationship developed by Doorenbos and Kassam (1979) (fig. 1), *p* is calculated as a function of potential plant transpiration (E_{pi}) by the fitted equation as:

$$p = -0.001\, E_{pi}^{\ 3} + 0.0228\, E_{pi}^{\ 2} - 0.2076\, E_{pi} + 0.9952 \tag{9}$$

The potential plant daily growth is adjusted with the water stress factor (WSF). It is defined as the ratio of actual available water content and potential available water in the soil:

$$\text{WSF} = \frac{\theta_a - \theta_{wp}}{\theta_{fc} - \theta_{wp}} \tag{10}$$

GRASIM distinguishes two horizontal soil layers of user−defined depths. Experimental evidence (Barnes et al., 1995; Miller, 1984) suggests that effective rooting depths for most common cool−season grasses are shallower than 1 m. Typically, most grass roots are found in the top 10 to 20 cm of the soil profile, and most forage crops have the bulk portion of their rooting systems above 70 cm depth in the soil. Thus, in this research, the maximum rooting depth for grass species is specified to be 70 cm, while the top soil layer is considered as 30 cm. Legume species such as red clover and alfalfa have deep taproot systems; thus, their effective rooting depths are defined as 1 m. It is assumed that each layer contributes half

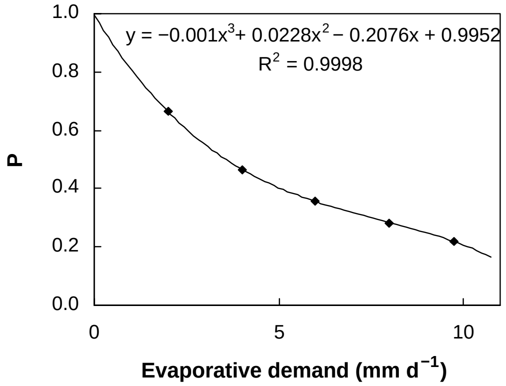

Figure 1. Relationship between the soil moisture depletion factor (*p*) and the evaporative demand (mm d^{-1}) for C$_3$ crop species (redrawn from Kropff, 1993, figure 5.4).

of the daily ET demand from a standing crop (Mohtar et al., 1997a).

Competition for Nutrients

GRASIM's soil nitrogen cycling component is based on the NLEAP model (Follett et al., 1991). The model accounts for daily nitrogen transformation in plants, soil, and water through processes of plant uptake, nitrification, denitrification, mineralization, volatilization, fertilization, and leaching. The nutrient module affects plant growth through the nitrogen stress factor and N uptake.

Plant daily nitrogen demand in GRASIM is estimated using a supply and demand approach as in the following equation:

$$\mathrm{NDMD} = \mathrm{YIELDG} \cdot \mathrm{TNU} \cdot \mathrm{FRACNU} \cdot \Delta\mathrm{T} \qquad (11)$$

where NDMD is the daily nitrogen demand (kg/ha); YIELDG is the yield goal for a crop (kg/ha); TNU is the total nitrogen uptake efficiency for a crop (kg N/harvest unit); FRACNU is a sigmoid function, with values ranging from 0 to 1 from start to end of a growing season, modifying the daily demand based on the relative crop growth stage in a growing season; and ΔT is the current model time step, which is one day in this case.

The same demand function (eq. 11) is used in the multispecies GRASIM to calculate N demand from each species. On a given day, the presence of each species is calculated as a percentage of its respective biomass in the total biomass of all species in the mixture. Then, the YIELDG for each species is reduced proportionally based on its percentage presence in the mixture; hence, the N demand by each species is reduced accordingly. In the new model, the default TNU value and FRACNU function are used for all forage species (Mohtar et al., 1997a). The effect of this model is that there is no direct competition among coexisting plant species in terms of nitrogen uptake, and all species have access to the available soil inorganic nitrogen pool according to their share in the mixture (Thornley, 1998; Rossiter and Riha, 1999; Herrero et al., 2000a, 2000b).

Daily total nitrogen demand of the mixed pasture is calculated by summing nitrogen demand of all species. The feedback from the nitrogen module to the plant growth module is the nitrogen stress factor (NSF), which is used to adjust daily potential plant growth. The NSF is calculated for each species as:

$$\mathrm{NSF}_i = \frac{\mathrm{NUPTAKE}}{\sum \mathrm{NDMD}_i} \qquad (12)$$

where NUPTAKE is the soil−available nitrogen for plant uptake including nitrate and ammonium nitrogen (Mohtar et al., 1997a), and NDMD_i is the plant demand for nitrogen uptake of the *i*th species when no nitrogen stress exists (Chen, 2000).

The equal access of soil nitrogen by all species described above and the NSF calculated by equation 12 are considered to address the indirect effect of plant species competition due to nitrogen availability (Kropff, 1993). To account for the direct effect of competition by coexisting species for a common nutrient, a growth reduction factor (YDRDFAC) is calculated based on the rationale proposed by Fresco (1985), who stated that the effect of scrambling for a common nutrient on plant growth is determined by the total nutrients available in the entire system and by the fraction of nutrients in standing crops:

$$\mathrm{YDRDFAC} = 1 - \frac{\sum p_i \mathrm{TDW}_i}{\sum p_i \mathrm{TDW}_i + \mathrm{Navail}_{soil}} \qquad (13)$$

where p_i is the percent nitrogen content of the *i*th species, TDW*i* is the total dry weight of the *i*th species, and Navail_{soil} is the current soil nitrogen content available for plant uptake. Both nitrogen stress factor (NSF) and the yield reduction factor (YDRDFAC) are within the range of 0 to 1 and are applied to adjust plant growth by multiplying the daily potential plant growth with the two factors. Since legume species can fix their own nitrogen, NSF and YDRDFAC are applied to adjust the potential growth of grass species only. Thus, daily growth of grass species is calculated as: grass actual growth = grass potential growth × NSF × YDRDFAC.

Biological Nitrogen Fixation

The growth, biological nitrogen fixation by the legume species, and the transfer of such fixed nitrogen to associated forage grass species have been well documented (Ledgard et al., 1985; Ta and Faris, 1987; Hutchings and Kristensen, 1995). Chen (2000) developed a legume module based on these findings and incorporated it into GRASIM. Daily legume potential growth is modified by a water stress factor (eq. 10) and a nitrogen inhibition factor (NIF) defined to vary from 0 to 1 to address the negative effect of N fertilization on legume growth, i.e., the greater the NIF value, the lower the inhibition on legume biomass production. Legume biological nitrogen fixation efficiency is defined as the atmospherically derived nitrogen fixation (kg) per ton of dry matter of legumes. It is influenced by the nitrogen fertilization rate in a hyperbolic fashion. Nitrogen fixation is also affected by water availability (positive) and years after establishment (decrease with sward age). The total bio−fixed nitrogen is the product of legume biomass, fixation efficiency, and a factor of 1.25 (Chen, 2000). The portion of the biologically fixed nitrogen that is transferred to associated grasses on a daily basis is calculated as the product of an empirically derived daily nitrogen transfer rate and the total bio−fixed nitrogen (Chen, 2000). Specifically, nitrogen transfer rate is defined for certain grass−legume combinations based on the observation made by Ta and Faris (1987).

FIELD EXPERIMENT

Grazing experiments were conducted at the Pennsylvania State University (PSU) Beef Research Farm in State College, Pennsylvania, to study the effect of grazing intensity on forage productivity. The experimental site is a ten−year−old mixed pasture that was formerly a perennial ryegrass and alfalfa, and orchardgrass and alfalfa hay experimental site. Soil series of the pasture is Hagerstown silt loam (fine, mixed, mesic, Typic Hapludalf).

The experimental design was a split−block with four replicates. Stocking intensity was controlled by the height of orchardgrass plants before and after stocking. Two grazing height regimes (treatments) were defined as: (1) tall grazing height (low stocking density) in which the mean orchardgrass height of the pasture was grazed from 27 cm down to 7 cm, and (2) short grazing height (high stocking density) in which the mean orchardgrass height of the pasture was grazed from 21 cm to 5 cm. Each grazing event was limited to 36 h or less. The experiment started in April 1998 and was repeated in 1999 with the same experimental design.

Two types of forage biomass data were collected before each grazing: forage harvested, and total herbage mass. Forage harvested data were collected by clipping pasture to 7 cm and 5 cm above ground in the tall and short grazing height treatments, respectively. Total herbage mass data were collected by clipping to ground level. After each data collection, forage samples were separated into different species groups and then dried and weighed to calculate the contribution of each species to the total herbage biomass. Biomass data for each species were compiled by averaging across all replicates over the two growing seasons to give rise to four data sets, which are labeled 1998 short, 1998 tall, 1999 short, and 1999 tall. In cases of incomplete total herbage mass and forage harvested data for a given species, the seasonal averaged harvest index (HI), defined as the ratio of forage harvested to total herbage mass, was used to construct the growth curve for that species (Carlassare and Karsten, 2002). In total, 30% of the data points were estimated with this method, and more than half of the missing data were for low abundance species, such as legumes and perennial rye grass. Species composition of the mixed pasture was dynamic and varied within and across growing seasons. When averaged across the two−year experiment, total herbage biomass was composed of 30% orchardgrass, 29% bluegrass, 17% quackgrass, 9% dandelion, and 7% legumes that included alfalfa, white clover, and red clover. Other minor species in the mixture were grouped as broadleaf (predominantly broadleaf plantain), perennial grasses (predominantly perennial ryegrass), and annual grasses (predominantly bromegrass).

Local weather data were collected for the two growing seasons, including daily minimum and maximum temperature (˚C) (figs. 2 and 3), rainfall (mm) (figs. 4 and 5), and solar radiation (W−min/m^2) (figs. 6 and 7). Detailed data collection procedures and analysis were published in an earlier article (Carlassare and Karsten, 2002).

MODEL EVALUATION

The multispecies GRASIM's ability to simulate the growth of competing forage species was evaluated by comparing model−simulated forage biomass to that measured for all species in the mixed pasture. The process involved model calibration of the plant growth parameters of GRASIM using 1998 data and the following validation simulation using 1999 data. Model calibration was done with a combination of numerical curve fitting and manual adjustment of the plant growth parameters based on the sensitivity analysis for GRASIM (Chen, 2000) to minimize the differences between simulated and observed growth curves for each species in the mixture. This process was conducted separately for the two grazing height treatments in the 1998 growing season, i.e., 1998 short and 1998 tall. The resulting calibrated plant growth parameter sets for the two treatments were then used for the two validation

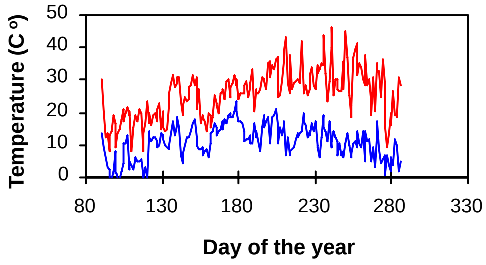

Figure 2. 1998 PSU daily minimum and maximum daily temperatures.

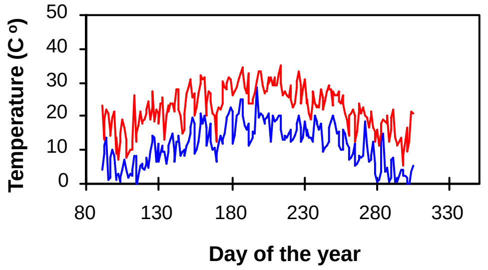

Figure 3. 1999 PSU daily minimum and maximum daily temperatures.

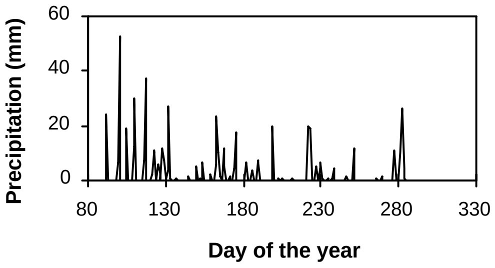

Figure 4. 1998 PSU daily rainfall.

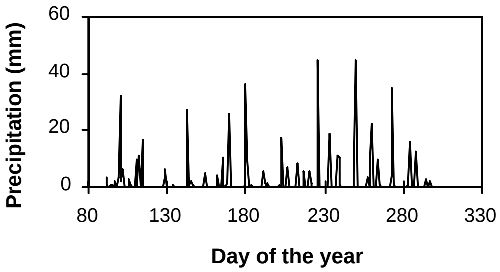

Figure 5. 1999 PSU daily rainfall.

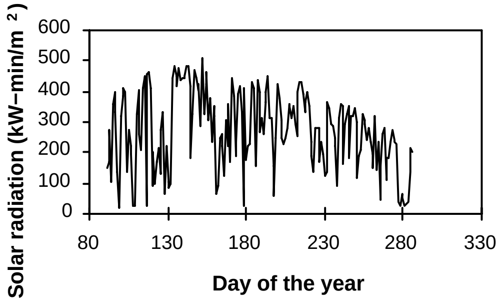

Figure 6. 1998 PSU daily solar radiation.

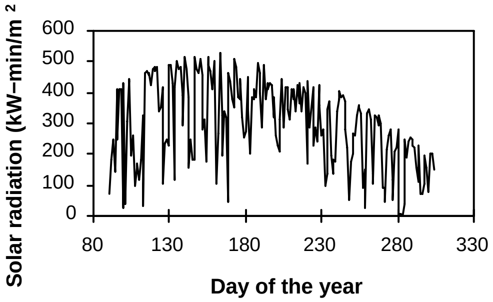

Figure 7. 1999 PSU daily solar radiation.

simulations of forage growth in the 1999 short and 1999 tall grazing height treatments, respectively.

Results and Discussion

The results of calibration of the multispecies GRASIM against 1998 short (high grazing intensity) and tall (low grazing intensity) treatment growth data are presented in figures 8a and 8b, respectively. In both calibration runs, the new model simulated reasonably closely the growth of multiple species in the pasture. Linear regression of measured vs. simulated biomass for all species gave a regression line with a slope of 0.98 and a *y*−intercept of 0.001 ($R^2 = 0.98$), which are not significantly different from 1 and 0, respectively. Noticeably, the new model underpredicted bluegrass growth during the early growing season and overpredicted it during the second half of the growing season. The simulated white clover growth follows its observed unimodal growth trend. For tall legumes, including alfalfa and red clover, the model simulated a unimodal growth pattern, which is different from the observed.

In the two validation simulations for the 1999 short and tall treatments, the model simulated similar growth trends to those observed for most species groups (figs. 9a and 9b). The regression line of observed vs. simulated values has a slope of 0.83 and *y*−intercept of 0.0008 ($R^2 = 0.97$) for the short treatment, and a slope of 0.92 and *y*−intercept of 0.003 ($R^2 = 0.98$) for the tall treatment.

Further examination of model performance was done through linear regression of measured vs. simulated biomass for each species in the calibration and validation simulations. The slopes and intercepts of regression lines and their coefficients of determination are listed in table 1. Overall, the dominant species including orchardgrass and quackgrass were more accurately simulated than low−incidence species including weeds (dandelion and broadleaf), legumes (tall legumes and white clover), and other minor annual and perennial grass species. In both calibration and validation simulations, the new model did not adequately simulate the growth dynamics of bluegrass, and it simulated a unimodal growth pattern for the tall legume species group with a decline of biomass during late seasons that is different from the observed data. Additionally, for low−incidence species, the new model generally performed better for simulating their growth in tall treatment than in short treatment, based on the coefficients of determination of the regression lines for these species, which are higher for tall treatment simulations than for short treatment simulations. For legume species, the new model performed poorer than it did on other grass species in all four simulations, judging by the lower coefficients of determination of the regression lines compared with those for other grass species (table 1).

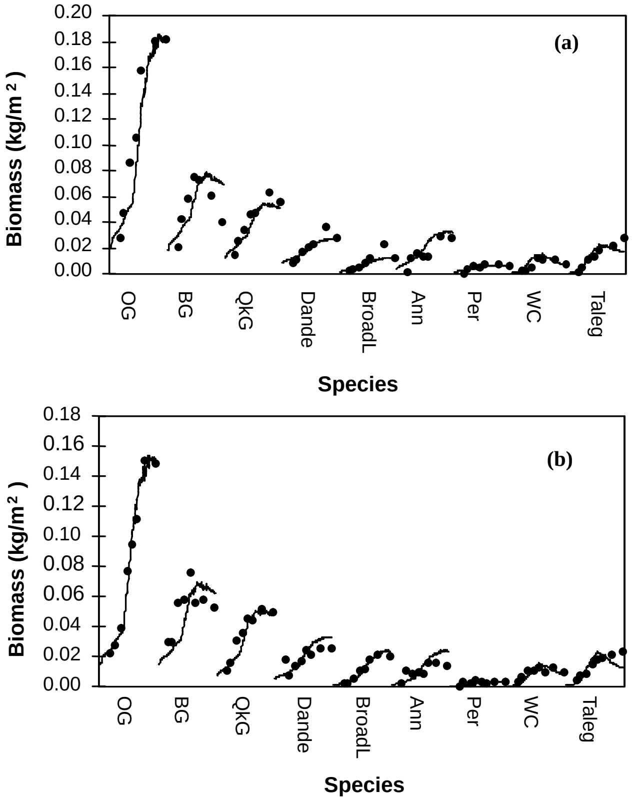

Figure 8. Simulated (lines) and measured (dots) growth curves for all species groups in calibration run for 1998 (a) short and (b) tall grazing height treatments. Data points for each species group are arranged sequentially following a leader label until the label for the next species group appears. Species group names are: OG = orchardgrass, BG = bluegrass, QkG = quackgrass, Dande = dandelion, BroadL = broadleaf, Ann = annual grasses, Per = perennial grasses other than OG and BG, WC = white clover, and Taleg = tall legumes including red clover and alfalfa.

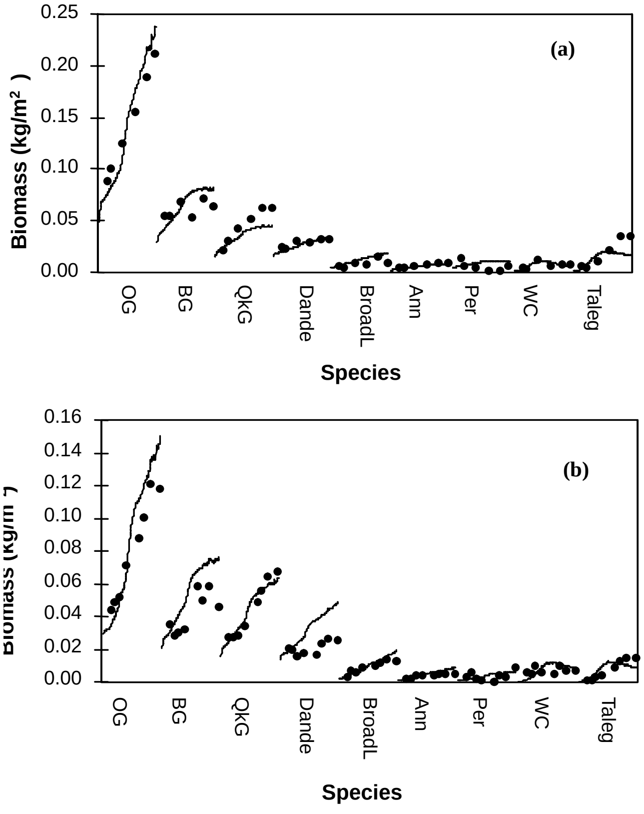

Figure 9. Simulated (lines) and measured (dots) growth curves for all species groups in validation run for 1999 (a) short and (b) tall grazing height treatments. Data points for each species group are arranged sequentially following a leader label until the label for the next species group appears. Species group names are: OG = orchardgrass, BG = bluegrass, QkG = quackgrass, Dande = dandelion, BroadL = broadleaf, Ann = annual grasses, Per = perennial grasses other than OG and BG, WC = white clover, and Taleg = tall legumes including red clover and alfalfa.

Table 1. Linear regression of observed vs. simulated biomass for all species groups for the two−year simulations. Regression line slope (b1), intercept (b0), and coefficient of determination (R^2) are shown.

	1998 (model calibration)						1999 (model validation)					
	Short Treatment			Tall Treatment			Short Treatment			Tall Treatment		
Species[a]	b0	b1	R^2	b0	b1	R^2	b0	b1	R^2	b0	b1	R^2
OG	0.0029	0.98	0.98	0.0136	0.98	0.94	0.0214[b]	0.68[b]	0.97	0.0394[b]	0.72[b]	0.98
BG	0.0239	0.60	0.55	0.0213	0.58	0.33	0.0103	0.58[b]	0.74	0.0455[b]	0.23[b]	0.25
QkG	0.0043	0.95	0.93	−0.0034	1.18	0.91	−0.0033	1.08	0.96	−0.0187[b]	1.78[b]	0.97
Dande	0.0081[b]	0.54[b]	0.71	−0.0073	1.46	0.88	0.0128[b]	0.25[b]	0.44	0.0139[b]	0.56[b]	0.77
BroadL	0.0012	0.88	0.95	−0.0021	1.59	0.77	0.0028[b]	0.60[b]	0.88	0.0027	0.50	0.53
Ann	0.0051[b]	0.43[b]	0.62	−0.00006	0.82	0.73	0.0017[b]	0.44[b]	0.74	0.0008	1.05	0.96
Per	0.0021	0.30	0.08	−0.0015	1.44	0.66	0.0018	0.48	0.10	0.0212[b]	−1.6[b]	0.65
WC	0.0046[b]	0.53[b]	0.73	0.0014	0.66	0.55	0.0063[b]	0.07[b]	0.02	0.0015	0.73	0.54
Taleg	0.0055	0.67	0.51	0.0004	0.97	0.65	−0.0013	1.15	0.58	−0.0022	1.49	0.48
Total	0.0473[b]	0.83[b]	0.97	0.0109	1.01	0.94	0.0484[b]	0.67[b]	0.96	0.0769	0.77	0.94

[a] OG = orchardgrass, BG = bluegrass, QkG = quackgrass, Dande = dandelion, BroadL = broadleaf, Ann = annual grasses, Per = perennial grasses other than OG and BG, WC = white clover, and Taleg = tall legumes including red clover and alfalfa.

[b] Denotes either that b0 is significantly different from 0 or that b1 is significantly different from 1 at $\alpha = 0.05$ significance level.

Linear regression of all measured biomass data on the simulated values for the two treatments across the two growing seasons gave a regression line with a slope of 0.95 and a *y*−intercept of 0.001 (R^2 = 0.97). Scatter plots of the measured versus simulated forage biomass for both tall and short treatments over two−year experiment shows that model predictions are reasonably close to observed growth of mixed pasture with a large number of coexisting species (fig. 10).

In the multispecies GRASIM, daily growth of every species is simulated based on the same set of processes converting daily solar radiation to carbon gain, while keeping its own set of growth parameters. GRASIM's plant growth module is physically based, and its parameters carry physiological meanings; thus, the calibration of these parameters under different scenarios could provide insight into forage growth under different management regimes. In this study, the calibrations of the short and tall treatment experiment in 1998 were done separately due to the important role of grazing or harvesting intensity in determining forage regrowth speed and pasture stand vigor.

Many researchers have found that low stubble height reduces the rate of regrowth after intensive grazing due to storage reserve depletion and lack of photosynthetic leaf area (Waller et al., 1985; Parsons et al., 1988; Williamson et al., 1989; Beuselinck et al., 1992). In this study, field data also indicated that moderate grazing intensity (taller stubble height) produced more available forage for the grazing animals than higher grazing intensity (shorter stubble height)

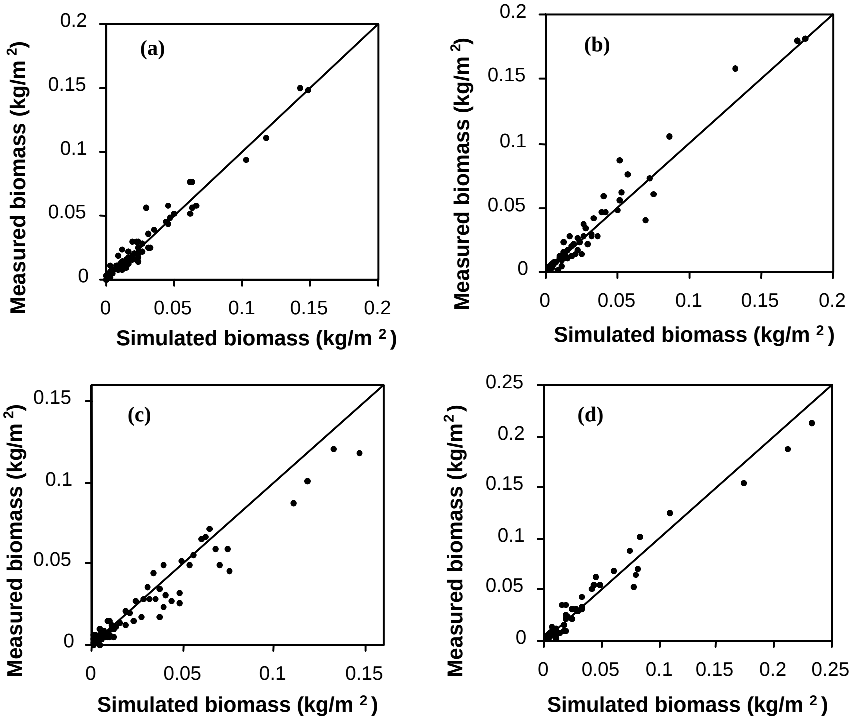

Figure 10. Observed versus simulated dry matter accumulation values for all species groups in mixed pasture in both tall and short treatments across 1998 and 1999 growing seasons: (a) 1998 short treatment (calibration), (b) 1998 tall treatment (calibration), (c) 1999 short treatment (validation), and (d) 1999 tall treatment (validation).

(Carlassare and Karsten, 2002). It is hypothesized that nonstructural carbohydrate reserve and residual leaf area were preserved more in tall stubble of the dominant species, such as orchardgrass, than in shorter stubble; this allowed faster regrowth and higher productivity in between grazing. The calibration process using 1998 short and tall treatment biomass data indeed suggested a combination of plant growth parameters with higher productivity potential for the tall grazing height treatment than those for the short grazing height treatment (table 2). For example, the dominant species, orchardgrass, had higher photosynthetic efficiency (α) and maximum specific growth rate (μ_m) in the tall treatment (low grazing intensity) than in the short treatment (high grazing intensity). Likewise, white clover and tall legume had greater μ_m in the tall treatment than in the short treatment (table 2).

In all four simulations, the multispecies model simulated a unimodal growth pattern for tall legume species that peaked at mid−season and then decreased quickly late in the season. This late−season decrease is not supported by the observed data (figs. 8 and 9). The simulated quick rise of tall legume species during early season is partly due to their higher canopy light extinction coefficient than those of the grasses (0.8 vs. 0.5 to 0.6 for other grass species in table 2), which is due to the more horizontal leaf angle typical of clovers and alfalfa. This gives the legume species the capability to capture more light with similar LAI, which coincides with the early season favorable growth conditions in general, i.e., relatively cooler temperatures, high level of solar radiation, and rainfall at spring time (figs. 2 to 7). This advantage is reinforced by the model assumption that there is no nitrogen stress for legume species due to their ability to biologically fix nitrogen. The late season rapid decrease could be due to the higher senescence rate assigned to legume species (table 2) to counteract the unreasonably high growth rate due to their higher light capture efficiency compared with their grass species counterpart. Although such high senescence rates for the legume species could be hypothesized to reflect, in part, the high diet preference and trampling damage by the grazing animals as observed by the field experiment implementers (Carlassare and Karsten, 2002), further detailed examination of the model theories regarding legume growth and its relation to grazing management is warranted.

The legume model for nitrogen fixation and transfer to associated grass was empirically developed based on the observed relationship between soil−available nitrogen and N_2 fixation. Chen (2000) tested the model using total biomass data of a binary mixture of orchardgrass and alfalfa grown at Logan, Utah, in 1997 and 1998. However, the ability of the model to simulate the detailed dynamics of individual species in the mixture was not tested. Nitrogen fixation and transfer rates are known to be influenced by moisture and temperature (Ranells and Wagger, 1996). Thus, the extrapolation of the empirical relations to other locations probably introduced additional uncertainties in the model predictions, which require more evaluation with independent studies.

Table 2. Calibrated plant growth parameters for each species group for the 1998 short and tall treatments, which were used for the simulation of the 1999 short and tall treatments, respectively.

Parameter[a]	Units	Species Groups[b]								
		OG	BG	QkG	Dande	Broad	Ann.	Per.	WC	Taleg
1998 Short Treatment										
sla	m^2/kg C	40	40	40	40	42	40	40	40	40
α	kg/CO$_2$/J	12E−9	12E−9	12E−9	12E−9	12E−9	12E−9	12E−9	10E−9	10E−9
k	−−	0.5	0.5	0.5	0.6	0.6	0.6	0.5	0.8	0.8
m	−−	0.12	0.12	0.12	0.12	0.13	0.12	0.12	0.12	0.12
γ	per day	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.08	0.08
β	per day	0.004	0.004	0.004	0.018	0.006	0.006	0.004	0.04	0.04
ϕ	−−	0.95	0.70	0.70	0.70	0.80	0.80	0.90	0.80	0.80
P_0	kg CO$_2$/m^2/s	5E−6	5E−6	5E−6	5E−6	5E−6	5E−6	5E−6	3E−7	5E−6
P_1	kg CO$_2$/m^2/s/c	5E−7	5E−7	5E−7	5E−7	5E−7	5E−7	5E−7	4E−6	5E−7
μ_m	per day	0.40	0.40	0.40	0.26	0.40	0.40	0.40	0.40	0.40
Rtdp	cm	70	70	70	70	70	70	70	70	100
1998 Tall Treatment										
sla	m^2/kg C	40	40	40	40	42	40	40	40	40
α	kg/CO$_2$/J	14E−9	12E−9	12E−9	12E−9	12E−9	12E−9	12E−9	10E−9	10E−9
k	−−	0.5	0.5	0.5	0.6	0.6	0.6	0.5	0.8	0.8
m	−−	0.12	0.12	0.12	0.12	0.13	0.12	0.12	0.12	0.12
γ	per day	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.08	0.08
β	per day	0.002	0.004	0.004	0.018	0.006	0.006	0.004	0.04	0.023
ϕ	−−	0.95	0.80	0.85	0.70	0.80	0.80	0.80	0.80	0.80
P_0	kg CO$_2$/m^2/s	5E−6	5E−6	5E−6	5E−6	5E−6	5E−6	5E−6	3E−7	5E−6
P_1	kg CO$_2$/m^2/s/c	5E−7	5E−7	5E−7	5E−7	5E−7	5E−7	5E−7	4E−6	5E−7
μ_m	per day	0.55	0.40	0.40	0.26	0.40	0.40	0.40	0.50	0.50
Rtdp	cm	70	70	70	70	70	70	70	70	100

[a] *sla* = specific leaf area, α = leaf photosynthetic efficiency, *k* = leaf extinction coefficient, *m* = leaf light transmission coefficient, γ = recycling constant, β = senescence constant, ϕ = photosynthate fraction partitioned to shoot, P_0 = light−saturated leaf photosynthetic rate constant, P_1 = light−saturated leaf photosynthetic rate coefficient, μ_m = maximum specific growth rate, and Rtdp = effective rooting depth. Sensitivity analysis (Chen, 2000) indicates that all growth parameters are effectively influential to GRASIM's prediction of forage biomass. It was found that ϕ is the most influential parameter, followed by α, *k*, *sla*, μ_m, γ, *m*, P_1, P_0, and β, with decreasing model sensitivity.

[b] OG = orchardgrass, BG = bluegrass, QkG = quackgrass, Dande = dandelion, BroadL = broadleaf, Ann = annual grasses, Per = perennial grasses other than OG and BG, WC = white clover, and Taleg = tall legumes including red clover and alfalfa.

Due to the high species diversity and spatial variability within the experimental pasture, as evident in many low nutrient and water input natural ecosystems (Mamolos et al., 1995), sampling errors were high, especially for low−incidence species (Carlassare, and Karsten, 2002). Occasionally, harvest index (HI), averaged across a growing season for a particular species group, was used to estimate missing data points for that species group. However, data from both 1998 and 1999 growing seasons suggested that species HI changed across seasons. Therefore, in many cases, the averaged HI was less than the actual proportion of available forage in the pasture for a given species (Carlassare and Karsten, 2002). This could also partially explain the tendency of the multispecies GRASIM to overpredict forage biomass, especially during the late season (figs. 8 and 9).

This work reveals several areas that could be improved in the interspecies competition modeling. First is the lack of linkage between plant growth and phenology. This is especially important in a mixed−species situation where certain species are not defoliated regularly by grazing animals or cutting, and in an agronomic cropping system where plants are left intact to complete a full lifecycle. Plant traits commonly vary to such an extent that a single “representative” value cannot adequately capture the detailed dynamics over a lifetime in such cases, thus introducing errors in model predictions.

Second, intercrop models tend to ignore spatial variability, which is typical under field conditions. In this research, the majority of the inconsistency within the dataset was due to the spatial heterogeneity in plant species distribution within the pasture. However, the sheer complexity and computing power required for a multi−dimensional models limit their development and application in real−world situations. Van Oene et al. (1999) proposed an ecosystem model for wetland plant and grazer simulation that employed a grid cell system to address the spatial distribution of plant species and animal grazing patterns. Although the model was not tested against observed data, it provided an example for dealing with this type of problem. There has been a trend to couple a geographical information system (GIS) with environment models to deal with the spatial variability. In light of this trend, a GIS interface was developed using ArcView for the multispecies GRASIM, through which users can link geo−spatial data and model output directly with a location for viewing and analysis (Zhai et al., 1999).

Third, modeling the canopy structure is typically simple in most intercrop models, and plant growth form is usually not explicitly modeled. Specifically, plant height should be included in the calculation of leaf distribution in a mixed canopy to more realistically simulate the partition of light within the mixture. In addition, the explicit modeling of forage height, stored organic reserve, and growth form could improve the model’s potential to explain the dynamics of regrowth mechanisms after cutting or grazing.

Lastly, species−specific growth interactions among coexisting species, such as the commonly noticed superior productivity of a certain mixture of legume and grass species compared to others, were not considered in this work. The explicit modeling of these types of interactions relies on the continuous and comprehensive study of various types of mixtures of species beyond simple yield testing experiments.

CONCLUSION

A new model was developed for simulating the growth and competitive interactions among coexisting species in a naturalized pasture. The original monoculture GRASIM was extended to simulate multiple species simultaneously by adding routines that describe the competition for light, water, and nitrogen. Partitioning of light was based on the estimated leaf area composition of the mixture. Regarding competition for soil moisture, each species group in the mixed pasture extracted water from a soil layer defined by its own effective rooting depth, and the extraction was driven by the solar radiation absorbed by the canopy of each species. Soil nitrogen was shared among coexisting species, and a reduction factor due to competition for nitrogen was applied to the growth of grass species. Legume species have the ability to biologically fix nitrogen and transfer nitrogen to associated grasses via root nodule decomposition and subsequent release of N.

In a two−year experiment at Pennsylvania State University, growth of a mixed pasture was measured under two stocking densities, and the forage data were used to calibrate and evaluate the model. The multispecies GRASIM reasonably simulated the relative trend and magnitude of biomass dynamics of major species, including orchardgrass, quackgrass, and dandelion, in the mixed pasture, judging by the high correlation coefficients of regression lines between measured and simulated biomass.

The modeling work also revealed several sources of errors in the simulations, and hence potential areas for future developments. Parameterization of the plant growth module of the new model revealed weakness in its simulation of legume species growth and lack of explicit modeling of plant growth form and canopy height distribution, which would perhaps lead to greater flexibility and power of a model in simulating plant growth dynamics more closely. Due to the naturally high degree of heterogeneity in the spatial distribution of plant species in a mixture, the model’s assumption of spatial uniformity in species distribution inevitably introduces modeling error, just as the sampling errors resulted from the generalization of point measurement of species composition to the entire field. The coupling of a GIS with the model to explicitly account for the spatial variance of both physical and biological environment could improve model performance. Additionally, as with many crop growth models, the multispecies GRASIM uses constant plant growth parameters for a given species. Therefore, it needs to relate the values of these parameters more closely to the phenology (growth stage) of a crop to address more closely the temporal heterogeneity of species composition in a mixed plant community. The new model could be the foundation of more detailed multispecies models for the development of useful tools in pasture and rangeland management.

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