Modeling Net Herbage Accumulation of an Orchardgrass Sward

M. Duru,* H. Ducrocq, C. Fabre, and E. Feuillerac

ABSTRACT

In order to simulate the effect of a wide range of defoliation regimes and levels of N supply on the net herbage accumulation of an orchardgrass (Dactylis glomerata L.) sward, we developed a model based on growth and senescence submodels. Four experiments (spring and summer regrowths), each comprising four treatments (two N rates × two amounts of residual biomass), were carried out to assess the effect of management on leaf growth, senescence, and radiation use efficiency (RUE). The growth submodel, based on RUE, depended on herbage N status and the development stage during stem elongation in spring. Increases in RUE during stem elongation depended on the percentage of reproductive tillers in the swards, which was a function of the N fertilizer rate. Leaf elongation and senescence rates at the tiller level and the mass per unit leaf area of green and senescent leaves were used to parameterize the senescence submodel. The amount of dead material depended mainly on the residual biomass at the beginning of regrowth. Complete calibration of the model was done using experiments and data from the literature. Other sets of experiments (one on orchardgrass and two others on permanent grasslands) were used for its validation. Root mean square errors for herbage yield were comprised between 11 and 55 g m⁻². The chosen model structure allows the growth of other grass species to be easily simulated, knowing their leaf life spans. However, this is a sink-driven model that is unable to assess tiller mortality and its effect on herbage accumulation rate.

Herbage accumulation is usually simulated for optimal defoliation management and high N fertilizer rates, which may be inappropriate for common farming practices in extensively farmed areas. There is a need to build a model having low N inputs and long regrowth period or residual sward mass. The model we built was designed to run in temperate oceanic areas where there is no or few water limitations for herbage growth. In this paper, the model is regarded as a heuristic management tool (Sinclair and Seligman, 1996), which means that it would be used to inform advisory services and farmers about the likely effects of grassland management scenarios on dry matter (DM) yield over a growing season so that these scenarios will be soundly based (Wilkins, 1995; Duru et al., 2000b). Because the use of models is often limited outside research groups (Donnelly and Moore, 1997), and in view of our aim, we chose a simple model that could be run as a spreadsheet. The model is based on C balance (Brisson et al., 1998), which is simpler than mechanistic models based on the balance between structural and metabolic C and N compartments (Sheehy and Johnson, 1988; Tabourel-Tayot and Gastal, 1998; Thornley, 2001), some of which run at a time step shorter than 1 d (Reido et al., 1998). This broad class of models, which includes a radiation interception submodel and another for the conversion of radiation into aerial biomass, has mainly been used for annual crops (Gosse et al., 1986). They have also been used for perennial grasses but only for frequent defoliation regimes or low residual herbage mass (Belanger et al., 1992; Gustavsson et al., 1995) where there was little or no senescence and no reproductive phase. Our objective was to extend the models to cover a wider range of management options and their interactions to roughly define, 1 to 5 mo ahead, how much area to allocate over a season by comparing different management options for defoliation intervals, late-cut hay (Theau et al., 2000), or variable residual sward mass (Duru et al., 2000b) and for a range of weather data.

(RUE) during crop growth is defined as the ratio of aboveground DM increase to the accumulated intercepted radiation following seed emergence (for annual crops) or defoliation (for grass swards). Usually, such a model should be coupled with a temperature-driven development submodel, simulating the formation and disappearance of sinks corresponding to changes in the trophic or morphological strategy of the crop, which influence the development of leaf area index (LAI) or grain filling (Brisson and Delécolle, 1991). Changes in aerial biomass are the result of different processes (leaf death, stem elongation, etc.) driven by the plant’s genetic makeup. Variation in RUE over time results from the sequence of these processes, which usually take place in the same order for a given crop. However, for perennial grasses, this is not the case because leaf senescence can begin immediately following defoliation for lenient (Len) grazing or several weeks later for severe (Sev) grazing (Parsons, 1988). Radiation use efficiency often takes a lower value after Len defoliation (Parsons et al., 2000), but this could be an artefact if the slower DM increase over time does not result from slower leaf growth but from higher leaf losses. Herbage senescence rate should be taken into account through a variable modifying the growth rate according to the residual sward state immediately after a defoliation (Parsons et al., 2001), or a senescence submodel should be added to a growth model for long period of regrowth or for reproductive phase as shown below.

As growth may be interrupted at any time, the stem elongation phase may or may not be concomitant with leaf senescence. For example, the heading stage often accompanies leaf senescence but only if there is no spring grazing. Spring grazing may delay the beginning of senescence for the following regrowth without any change in reproductive events (Gillet, 1980). For this reason, growth during stem elongation should be mod-

Abbreviations: DD, degree-days; DM, dry matter; Len, lenient (defoliation); LAI, leaf area index; Ni, sward nitrogen index; PAR, photosynthetically active radiation; RMSE, root mean square error; RUE, radiation use efficiency; Sev, severe (defoliation); SLA, specific leaf area.
eled separately from leaf senescence. A development submodel that runs during the reproductive phase (stem elongation, flowering time) should be added to take account of this change in the crop’s growth behavior. In fact, there is an increase in RUE over the stem elongation period that is not due merely to the temperature increase (Garcia et al., 1988).

When the sward is submitted to frequent and intense defoliation, processes of storage and remobilization of C and N can have a considerable effect on growth rate and sward structure (tiller density) following defoliation (Richards, 1993). Given their potential effect on tiller death and leaf growth following defoliation, these processes must be taken into account using a model driven by both source and sink (Schapendonk et al., 1998). To make sure that the variation over time in leaf yield was the result of both growth and senescent fluxes, we compared the dynamics of net herbage growth in terms of mass and length. At each date, the difference between the accumulated length of growing lamina and the standing green lamina was used to calculate the senescent and dead part. Second, we compared the RUE of treatments differing in their residual herbage mass, hypothesizing that treatments having high residual mass would have too low an RUE due to high senescence.

To build the senescence submodel, the principle chosen consisted of subtracting from the growth of leaves that are completely senescent, and we assumed that these dead leaves are not part of the yield. The parameters to be estimated were the proportion of DM that is remobilized before the leaf becomes completely senescent ($\lambda$) and the leaf’s life span. Remobilizations were defined from the ratio of green specific leaf area (SLAg) to that of the completely senescent leaves (SLAs): $\lambda = 1 - (\text{SLAg}/\text{SLAs})$. Leaf turnover, which depends on leaf life span, should be expressed in accumulated degree-days (DD) because we show that in this way, it was less variable between growing seasons than if expressed in days (Duru et al., 1993). Following complete defoliation, leaf losses begin once the first leaf to appear has completed its life span. In the case of incomplete defoliation, the losses begin immediately following defoliation. We assumed that leaf mass losses ($W_s$, g m$^{-2}$) were an increasing function of the residual herbage mass following a defoliation ($W_0$, g m$^{-2}$) according to the following equation:

$$W_s = W_0 \times (1 - \lambda) \times \Sigma \Theta/L$$  \[5\]

where $\Sigma \Theta$ is the time (DD) elapsed since the last defoliation and $L$ is the leaf lifespan (DD).

From a trophic point of view, the reproductive sward in spring has a far greater potential for photosynthesis than the vegetative sward in summer (Parsons, 1988) because flower stem extension keeps developing leaves in the zone of high irradiance near the top of the canopy, unlike vegetative swards (Woledge, 1978, 1979). After stem extension, it decreases because leaf appearance ceases on the flowering tillers. This trophic change, which leads to an increase in RUE during stem elongation (Bélanger et al., 1994), was expressed by a coefficient $(1 + \alpha)$. We assumed that this increase is proportional to the fraction of reproductive tillers: $\alpha$ should be maximal if a large proportion of tillers is reproductive or nil if vegetative. The proportion of reproductive tillers depends mainly on N supply (Duru et al., 2000a). We therefore assumed that the increase in potential for photosynthesis was maximal ($\alpha = 0.65$, after Woledge, 1979) when N was nonlimiting for herbage growth ($N_i = 100$) and was zero with severe N deficiency ($N_i = 40$) (Duru et al., 2000a).

$$\text{RIE}_j = 0.95 (1 - e^{-K \times \text{LAI}_j})$$  \[2\]

The cumulative intercepted photosynthetically active radiation ($\Sigma \text{PAR}$), from a cut ($j = 1$) to a sampling date ($d$), was computed from radiation measurements and RIE:

$$\Sigma \text{PAR} = \sum_{j=1}^{d} 0.48R_a \times \text{RIE}_j$$  \[3\]

where $R_a$ is daily total radiation on day $j$ in MJ.

As shown in the literature (Sinclair and Horie, 1989), the RUE (g MJ$^{-1}$ DM) depends on the N rate; it was expressed as a linear function of N (Bélanger et al., 1992):

$$\text{RUE} = a \times N_i + b$$  \[4\]

The purpose of the present study is to develop a senescence submodel over the vegetative and reproductive phases and a growth submodel over the reproductive phase. Experimental results for grass swards without any water limitation are presented in the second section. In the last section, we use these data to parameterize the model. We then carry out a complete validation.

**MATERIALS AND METHODS**

**Structure of the Model**

For modeling herbage accumulation in the absence of senescence, four relationships among variables were required. Two equations were specially calibrated (Eq. [1] and [4]) while the others were derived from the literature. The parameters of Eq. [1] and [4] have to be estimated.

Leaf growth depends mainly on temperature and N (Gastal et al., 1993). Given their potential effect on tiller and sward structure (tiller density) following defoliation, the sink effect should be small (Schnyder et al., 2000).

In this paper, we only consider a source-driven model of both growth and senescent fluxes, we compared the dynamics of net herbage growth in terms of mass and length. At each date, the difference between the accumulated length of growing lamina and the standing green lamina was used to calculate the senescent and dead part. Second, we compared the RUE of treatments differing in their residual herbage mass, hypothesizing that treatments having high residual mass would have too low an RUE due to high senescence.

The aim of this study was to build a simple model of net herbage accumulation during spring and summer for grass swards submitted to a wide range of N rates and defoliation regimes, particularly in late spring when swards are reproductive and for high residual herbage mass after defoliation in both seasons. The first section describes the structure of the model and the experimental design used for model calibration. There were three submodels. The growth submodel for the vegetative phase had the same main features as previously published models (e.g., Bélanger et al., 1992). The purpose of the present study is to develop a senescence submodel over the vegetative and reproductive phases and a growth submodel over the reproductive phase. Experimental results for grass swards without any water limitation are presented in the second section. In the last section, we use these data to parameterize the model. We then carry out a complete validation.

$$\text{LAI}_j - \text{LAI}_{j-1} = a \times N_i \times (b \times \Theta + c \times \Theta^2)$$  \[1\]

where $j$ is the day, $N_i$ = herbage N index (see Data Analysis subsection for calculation), and $\Theta$ = average daily temperature.

The radiation interception efficiency (RIE) depended on the LAI. The extinction coefficient ($K$) was taken to be 0.52 for spring growth and 0.56 for summer regrowth (Varlet-Grancher et al., 1989):
For the development submodel, three key dates had to be defined. The first was when to initialize the model. Once flower induction begins, the onset of reproductive growth at the shoot apex generally depends on a period of exposure to long photoperiods. Spring temperatures may accelerate or delay the development of the inflorescence (Robson et al., 1988). The double-ridge stage, which is the first unequivocal sign that the shoot is in transition to reproduction, was used to initialize accumulated temperatures. It corresponds to an increase in leaf elongation rate (Parsons, 1988). The time at which this stage occurs depends mainly on latitude (Peacock, 1975) but only a little on species and cultivar. For orchardgrass, it may occur from the middle of January until the middle of February according to location (Niqueux and Arnaud, 1967; Duru et al., 2000a).

We chose the 1 February as an average date. The second and third dates (the beginning and the end of stem elongation, respectively) can be assessed from the accumulated daily temperatures (Niqueux and Arnaud, 1967). We assumed that the increase in RUE begins with stem elongation and reaches its maximum value when stem elongation is finished.

### Study of the Effect of Nitrogen Application and Defoliation Regime on Net Herbage Accumulation

#### Experimental Design

The study was conducted on a clay loam soil near Toulouse (48° 70' N, 1.2° E; altitude 200 m above sea level). Swards of orchardgrass ('Lude') were sown in autumn 1993. Studies were done in 1995 and 1996 (spring growth, which was reproductive) and in 1994 and 1997 (vegetative regrowth in summer); each regrowth was subjected to two defoliation regimes and two levels of applied N (Table 1). The two cutting regimes mimicked the pattern of grass regrowth, following a Len or Sev defoliation. The Sve plots were completely defoliated immediately before the first date of measurement of herbage DM accumulation. The Len plots had not been cut for 3 wk (summer regrowth in 1994 and 1997) or since the previous autumn (spring growth in 1995 and 1996). The Len plots were not defoliated when the Sve plots were completely defoliated. We assumed that at this time, they were virtually defoliated. In this way, what we called residual sward characteristics were observed just after the cut for the Sve treatments but 3 wk or more after the last cut on Len treatments. Nitrogen was applied at the second cutting date, except in 1994. The four treatments were arranged in a randomized block design with four replications. Measurements were made each year at different positions in the sward. Plot size was 4 by 5 m. There was no water limitation during spring growth. For summer regrowth, plots were irrigated when necessary to prevent any water stress. Average daily temperatures over the study period are given on Table 1.

#### Measurements

The biomass of aerial parts was measured from 7 to 10 randomly chosen subplots of 0.25 m², cut at 1 cm above ground level with a small clipping machine. Litter that was on the ground was not included in the yield. On a subsample of herbage, green and senescent laminae were separated from sheath, stem, and inflorescence. On a subsample of green laminae (about 500 cm²), the area of individual laminae was measured (LI 3000, LI-COR, Lincoln, NE) to calculate the LAI and the specific leaf area (SLA) on green lamina. Furthermore, SLA was measured on senescent laminae in 1995 and 1996. Plant components were dried at 80°C for 48 h and milled through a 0.8-mm screen. Total N concentration was measured at each date on the nonsorted subsample by a Kjeldahl procedure (Anonymous, 1985). Tiller density was measured four or five times during the experimental period by mass, weighing 50 tillers chosen at random from a subplot of 0.25 m², instead of counting. From herbage collected on each subplot, we selected 100 tillers at random and sorted them into vegetative and reproductive (shooting or heading stages). For reproductive tillers, the sheath length was measured from the bottom of the stem up to the ligule of the youngest leaf. At the tiller level, 20 individual marked tillers within the sward were identified in each plot, i.e., 80 tillers per treatment, with a plastic ring to measure the total length and the green part of each mature and growing lamina once a week (1994 and 1997) or every 10 d (1995 and 1996).

#### Data Analysis

Leaf appearance and expansion rates were expressed in DD (0°C basis) rather than in days, in view of the dominant effect of temperature on the morphogenetic process (Galagher, 1979). Leaf life span was calculated, once over a growth cycle, as the difference between two dates, d₂ and d₁. We chose d₂ as the last measurement date in a growing cycle, and d₁ was the date earlier than d₂ when all of the leaf was green or partially green. Measurements of leaf appearance, length, and death at the tiller level allowed growth and senescence rates in length to be accurately assessed.

### Table 1. Definition of treatments for model calibration.

<table>
<thead>
<tr>
<th>Growing season</th>
<th>Cutting dates to set up the experiment</th>
<th>N supplied, kg ha⁻¹</th>
<th>Studied period (average daily temperatures, °C)</th>
<th>Treatment code</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>4 June†</td>
<td>120 (4 June)</td>
<td>4 June–21 July</td>
<td>S1</td>
</tr>
<tr>
<td></td>
<td>4 June</td>
<td>120 (12 May)</td>
<td>4 June–21 July</td>
<td>S0</td>
</tr>
<tr>
<td></td>
<td>12 May</td>
<td>0</td>
<td>4 June–21 July</td>
<td>S0</td>
</tr>
<tr>
<td></td>
<td>12 May</td>
<td>0</td>
<td>4 June–21 July</td>
<td>S0</td>
</tr>
<tr>
<td>1995</td>
<td>5 Feb.†</td>
<td>120 (5 Feb.)</td>
<td>9 Feb.–31 May</td>
<td>S1</td>
</tr>
<tr>
<td></td>
<td>5 Feb.</td>
<td>0</td>
<td>9 Feb.–31 May</td>
<td>S0</td>
</tr>
<tr>
<td></td>
<td>7 Oct. 1994</td>
<td>120 (5 Feb.)</td>
<td>9 Feb.–31 May</td>
<td>S0</td>
</tr>
<tr>
<td></td>
<td>7 Oct. 1994</td>
<td>0</td>
<td>9 Feb.–31 May</td>
<td>S0</td>
</tr>
<tr>
<td>1996</td>
<td>16 Feb.†</td>
<td>120 (16 Feb.)</td>
<td>16 Feb.–22 May</td>
<td>S1</td>
</tr>
<tr>
<td></td>
<td>16 Feb.</td>
<td>120 (16 Feb.)</td>
<td>16 Feb.–22 May</td>
<td>S0</td>
</tr>
<tr>
<td></td>
<td>5 Oct. 1995</td>
<td>120 (16 Feb.)</td>
<td>16 Feb.–22 May</td>
<td>S0</td>
</tr>
<tr>
<td></td>
<td>5 Oct. 1995</td>
<td>0</td>
<td>16 Feb.–22 May</td>
<td>S0</td>
</tr>
<tr>
<td>1997</td>
<td>4 June†</td>
<td>120 (4 June)</td>
<td>4 June–15 July</td>
<td>S1</td>
</tr>
<tr>
<td></td>
<td>4 June</td>
<td>120 (4 June)</td>
<td>4 June–15 July</td>
<td>S0</td>
</tr>
<tr>
<td></td>
<td>12 May</td>
<td>10</td>
<td>4 June–15 July</td>
<td>S0</td>
</tr>
<tr>
<td></td>
<td>12 May</td>
<td>0</td>
<td>4 June–15 July</td>
<td>S0</td>
</tr>
</tbody>
</table>

† Dates when residual herbage mass and residual lamina length were measured for each of the four treatments.
so that net lamina length could be found from the difference between these two rates.

As the different N supplies led to rates of N uptake that differed according to the growing season, we used indices of herbage N status to accurately compare the different treatments. Plant N status was assessed from its concentration in the herbage and biomass. Optimum herbage N concentration for C₃ species is $N = 4.8(1000 \times W)^{-0.32}$ (Lemaire and Gastal, 1997), with $W$ and $N$ being the aerial biomass (kg ha$^{-1}$) and the N concentration in the herbage (% DM), respectively.

To assess the N status in suboptimal conditions, we used this relationship, calculating an index (Ni) as the ratio between the measured N concentration (Nm) of the harvestable shoot biomass ($W$) and the optimum N concentration as previously defined (Lemaire and Gastal, 1997):

$$Ni = \frac{100Nm}{[4.8(1000 \times W)^{-0.32}]}$$  

[7]

Usually, the Ni varied from 30 to 120, 100 indicating no N limitation of growth (Lemaire and Gastal, 1997). We computed the average daily increase in LAI, and then stepwise regression was used to relate it to the Ni, the average daily temperature, and its square. We considered only the Sever treatment and a growth duration of less than 700 DD to avoid the senescent phase (Duru et al., 1993). Analysis of variance was carried out separately for each growing season to compare the effect of fertilizer treatments and cutting regimes on leaf growth, death,sla, and tiller characteristics.

### Model Validation

The test of an engineering model such as this (Passioura, 1996) is its ability to mimic the effects of a wide range of input variables (e.g., weather, nutrient availability, and frequency and intensity of defoliation). Three databases were used.

The first came from experiments carried out on orchardgrass at Toulouse. Vegetative growth (two growing seasons) and reproductive growth (five growing seasons) were validated separately. Validation included the Len treatments of the 1995 and 1996 experiments because these data were not used for model calibration (Table 2). We regressed measured and simulated herbage mass and computed root mean square error (RMSE). The two other databases were created from records of herbage mass from permanent grasslands on commercial farms. They were composed mainly of grasses [at least 30% orchardgrass and other grasses such as perennial ryegrass (Lolium perenne L.) and velvetgrass (Holcus lanatus L.)] and few dicotyledons, all of the dominant species having the same growth strategy for resource capture (Grime, 2001). Herbage mass was the whole herbage, all of the species being weighed together. Over the studied period, there was no limitation by water for herbage growth, according to computations from rainfall, soil water capacity, and evapotranspiration. One database concerned a set of permanent grasslands (Theau et al., 2000) used mainly for hay in the French Pyrenees (42°48' N, 0°30' E; 750 m above sea level) (Table 2). The other concerned a set of orchardgrass swards and permanent grasslands in Segala (49°15' N, 0°30' E; 650 m above sea level) used for rotational grazing by dairy ewes (Ovis aries) and cows (Bos taurus) (Duru et al., 2000b) (Table 2).

This validation was comprehensive because it focused both on the framework and on the different parameters of the model. Apart from weather data, the other input variable was the herbage N status. Leaf life span and limits of stem elongation for the reproductive regrowths were assessed for orchardgrass. The same values were considered for the permanent grasslands in the Pyrenees and in the Segala.

#### RESULTS OF EXPERIMENTS AND MODEL CALIBRATION

### Herbage Nitrogen Status and Net Herbage Accumulation

The herbage N status was always significantly lower for the treatments where no N was applied (Table 3). Nitrogen indices tended to decrease with time within each experimental period, particularly when N was applied (data not shown). Tiller density was significantly increased when N was applied, except on the Len treatment in 1995 (Table 3). It did not vary significantly at the different sampling dates, except in 1996 when the coefficients of variation were highest (68 and 84% in 1996 for the Len treatments). For these treatments, which were not cut in February 1996, the tiller density fell from the beginning of February to the beginning of April by 38 and 64% (data not shown) with and without N application, respectively.

Dry matter yield reached about 800 g m$^{-2}$ DM for the spring growth but did not exceed 600 g m$^{-2}$ for summer regrowth (Fig. 1). However, the net rate of DM increase was the fastest in summer because the regrowth

### Table 2. Characterization of treatments on orchardgrass swards (Toulouse) and permanent grasslands (Pyrenees and Segala) used for model validation.

<table>
<thead>
<tr>
<th>Year</th>
<th>Location and period</th>
<th>Number of treatments (Toulouse) or plots (Pyrenees and Segala)</th>
<th>Last cut before beginning of measurement or grassland management</th>
<th>First and last dates of measurements</th>
<th>Accumulated temperatures† (degree-days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>Toulouse in spring</td>
<td>2‡ (100, 70)§</td>
<td>20 Mar.</td>
<td>22 Mar.–10 May</td>
<td>90–592</td>
</tr>
<tr>
<td>1990</td>
<td>Toulouse in summer</td>
<td>4‡ (97, 86, 71, 49)</td>
<td>23 Oct. and 20 Feb.</td>
<td>20 Feb.–9 May</td>
<td>101–892</td>
</tr>
<tr>
<td>1991</td>
<td>Toulouse in summer</td>
<td>2‡ (94, 78)</td>
<td>17 May</td>
<td>17 May–15 July</td>
<td>144–1086</td>
</tr>
<tr>
<td>1992</td>
<td>Pyrenees in spring</td>
<td>4‡ (87, 85, 74, 60)</td>
<td>18 May and 6 June</td>
<td>25 May–15 July</td>
<td>126–1026</td>
</tr>
<tr>
<td>1998</td>
<td>Pyrenees in summer</td>
<td>72 (from 48 to 82)</td>
<td>Grazing in autumn for ungrazed plots in spring; from 20 Apr. to 14 May for grazed plots in spring</td>
<td>28 Apr.–1 July</td>
<td>588–879 (early spring yield)</td>
</tr>
<tr>
<td>1993</td>
<td>Segala in spring</td>
<td>67 (from 51 to 100)</td>
<td>From three to five grazing cycles per plot</td>
<td>23 Mar.–30 June</td>
<td>70–388</td>
</tr>
<tr>
<td>1994</td>
<td>Segala in summer</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

† Minimum and maximum observed accumulated temperatures from 1 February (spring growth) or from the first date of measurement (summer regrowth) up to the first and the last date of measurement (Toulouse and Pyrenees) or accumulated temperatures between two grazing episodes (Segala).

‡ Two N treatments.

§ Average herbage N indices.

¶ Two cutting regimes that mimicked the pattern of grass regrowth, following lenient (last cut in autumn) and severe (last cut in spring) defoliation, respectively, combined with two N treatments.
interval was about half that found in spring. For the L1 treatment, there was a ceiling yield for the four regrowths. At the end of the experimental period, N fertilizer always significantly increased herbage yield by about 25% (1997) up to more than 300% (1996). The Len cutting treatment led to an increase in DM yield, which was not significant for treatments with N applied in 1995 and in 1996 but was significant and greater than 25% in 1994 and in 1997. For spring growth, there was a substantial increase in herbage DM yield around Day 25% in 1994 and in 1997. Furthermore, differences between regrowths (1994 and 1997). Furthermore, differences between regrowths when the temperatures were highest (1994 and 1997). The death/growth ratio was always much lower for the Sev treatments (1994, 1995, 1996, and 1997), than for treatments with N applied (0) of N fertilizer. There was a highly significant effect of N fertilizer on leaf growth and death rates and of defoliation regime on leaf death rate. The proportion of dead leaves was always greater for the Len treatments (Table 4). This means that the Len cutting management increased the dead leaf fluxes more than the leaf growth fluxes because of the higher residual leaf length (Table 3). The lamina length was closely correlated with green lamina mass for all of the treatments of a given regrowth. For every regrowth, N application always increased growth more than senescence so that the netThis increase ... that the effect of temperature was on treatment and growing season (Table 4). For a given

Table 3. Characterization of orchardgrass sward for the defoliation and N treatments (D and N, respectively): herbage N index, residual sward state, and tiller density over the regrowth interval. Values are means (M) ± standard error (SE).

<table>
<thead>
<tr>
<th>Growing season</th>
<th>Treatment code†</th>
<th>Average herbage N index</th>
<th>Residual lamina length</th>
<th>Tiller density (CV)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Significance of treatments</td>
<td>M ± SE</td>
<td>N</td>
<td>D</td>
</tr>
<tr>
<td>1994</td>
<td>S1</td>
<td>87 ± 4</td>
<td>*** NS§</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>S0</td>
<td>44 ± 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L1</td>
<td>73 ± 3</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L0</td>
<td>42 ± 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td>S1</td>
<td>87 ± 2</td>
<td>*** NS</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>S0</td>
<td>37 ± 1</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>L1</td>
<td>90 ± 3</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>L0</td>
<td>55 ± 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td>S1</td>
<td>97 ± 2</td>
<td>*** NS</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>S0</td>
<td>36 ± 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L1</td>
<td>97 ± 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L0</td>
<td>50 ± 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>S1</td>
<td>92 ± 5</td>
<td>*** NS</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>S0</td>
<td>55 ± 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L1</td>
<td>96 ± 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>L0</td>
<td>66 ± 1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Significant at P < 0.05.
** Significant at P < 0.01.
***Significant at P < 0.001.
† L and S were two cutting regimes that mimicked the pattern of grass regrowth, following lenient and severe defoliation, respectively, with application (1) or no application (0) of N fertilizer.
‡ CV, coefficient of variation through the different sampling dates.
§ NS, nonsignificant.
Fig. 1. Herbage accumulation for the four growing seasons and the four treatments; vertical bars indicate standard error of 1.

Fig. 2. Leaf area index (LAI) plotted against accumulated degree-days for treatments with severe defoliation and N application or nil for summer regrowths and spring regrowths; vertical bars indicate standard error of 1.
The SLA of the senescent fractions was significantly higher than for green leaves in every growing season, except in 1995 for Len treatments. The difference between the two fractions varied from 2 to 24%, depending on year and treatment (Table 5). Greatest differences were observed for the S0 treatment, which had the lowest herbage N status.

Stem length of reproductive tillers increased from about 650 DD in both growing seasons. For the selected tillers that were a mixture of vegetative and reproductive tillers, lamina length increased up to the end of the studied period (Fig. 3). At the same time, lamina length of reproductive tillers increased linearly until about 900 DD, after which lamina growth stopped (not shown).

### Herbage Accumulation and Radiation Use Efficiency

During the vegetative phase, the slopes of the curves of net aerial DM accumulation against accumulated intercepted radiation were different, depending mainly on the fertilizer treatment (Fig. 4). Differences in slopes between the N treatments were greatest for the Sev defoliation regime. At the beginning of regrowth, we observed a decrease in herbage mass for the Len treatments in spring, particularly for L0 in 1996.

For each of the treatments, RUE was computed using only data recorded before the first leaf to appear on Sev treatments had become completely senescent or before stem elongation began on spring regrowths. Moreover, we did not retain the first measurement on year and treatment (Table 5). Greatest differences were observed for the S0 treatment, which had the lowest herbage N status. The SLA of the senescent fractions was significantly higher than for green leaves in every growing season, on the fertilizer treatment (Fig. 4). Differences in slopes between the N treatments were greatest for the Sev treatments.

### Table 5. Comparison of specific lamina area of green and senescent parts of an orchardgrass sward subjected to two defoliation and two N treatments. Values are means ± standard error.

<table>
<thead>
<tr>
<th>Growing season</th>
<th>Treatment†</th>
<th>Green part</th>
<th>Senescent part</th>
<th>Specific lamina area</th>
<th>Comparison of green and senescent parts</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Significance</td>
</tr>
<tr>
<td></td>
<td></td>
<td>m² g⁻¹</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td>S1</td>
<td>26 ± 1</td>
<td>30 ± 2</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>S0</td>
<td>18 ± 1</td>
<td>24 ± 1</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>L1</td>
<td>29 ± 2</td>
<td>30 ± 2</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>L0</td>
<td>22 ± 1</td>
<td>23 ± 1</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td>1996</td>
<td>S1</td>
<td>23 ± 2</td>
<td>25 ± 1</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>S0</td>
<td>18 ± 1</td>
<td>21 ± 1</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>L1</td>
<td>23 ± 1</td>
<td>25 ± 2</td>
<td></td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>L0</td>
<td>17 ± 1</td>
<td>19 ± 1</td>
<td></td>
<td>NS</td>
</tr>
</tbody>
</table>

* Significant at P < 0.05.
** Significant at P < 0.01.
*** Significant at P < 0.001.
† L and S were two cutting regimes that mimicked the pattern of grass regrowth, following lenient and severe defoliation, respectively, with application (1) or no application (0) of N fertilizer.
‡ (senescent – green) × 100/green.
mass (see legend of Fig. 5). It shows that net herbage accumulation rate was lower for Len than for Sev treatments because of leaf losses occurring when there was residual herbage mass. For example, RUE was 0.38 g MJ⁻¹ DM less on the Len treatments compared with the Sev treatments when herbage N status = 50.

During stem elongation, RUE was greater than 2 g MJ⁻¹ DM when radiation interception efficiency was maximum (after Fig. 4). Using only the stem mass to calculate RUE, we found that it was correlated with the proportion of reproductive tillers observed during the stem elongation phase, which varied from 10 to 77%, mainly depending on the N treatment (see Table 6 for Len treatments in 1995 and 1996) ($r^2 = 0.69, P < 0.01$).

Computed only from stem mass, RUE was correlated with the herbage Ni:

$$
RUE = 0.023Ni - 0.15, \quad r^2 = 0.66, \quad P < 0.01, \quad \text{and}
$$

$$
SE = 0.16
$$

[9]

These parameters were close to those found for vegetative regrowths, leading to a superposition of both fitted curves (those on Sev treatment in Fig. 5 and those computed from Eq. [9]). We concluded that if there was no leaf death during the stem elongation phase, RUE should be greater than that calculated for vegetative swards.

### MODELING AND VALIDATION

#### Choice of Submodels and Parameters for Herbage Accumulation Modeling

The fact that green lamina mass was closely correlated with lamina length for all of the treatments of a given regrowth means that green lamina mass at the sward level was a fair indicator of green lamina length per tiller resulting from growth and senescence rates. This confirms that the fraction of dead lamina that could reach 90% of the lamina length (Table 4) had really affected the net herbage accumulation rate, which confirms that it was fully justified to consider both a growth and a senescence submodel.

Concerning the growth submodel, because crop growth and intercepted radiation (PAR) are always closely correlated and because both of them were cumulated, mean- light interception is not always the major factor limiting crop growth (Demetriades-Shah et al., 1992), we computed the RUE on a weekly (summer regrowth) or 10-d (spring regrowth before stem elongation) scale ($d_2 - d_1$), taking account of the herbage N status, for Sev treatments:

$$
RUE = (DM_{d_2} - DM_{d_1})/(PAR_{d_2} - PAR_{d_1}) \times Ni
$$

[10]

We found that $RUE = 0.018Ni$, $r^2 = 0.75$. This value

### Table 6. Proportion of orchardgrass reproductive tillers in spring for treatments with and without N fertilizer supplied at Toulouse. Values are means ± standard error.

<table>
<thead>
<tr>
<th>Growing season</th>
<th>N fertilizer and defoliation management</th>
<th>With N application</th>
<th>Without N application</th>
<th>Significance of the N treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>N applied in spring, last cut before measurement in February</td>
<td>3 ± 1</td>
<td>1 ± 1</td>
<td>NS</td>
</tr>
<tr>
<td>1991</td>
<td>N applied in spring, last cut before measurement in February</td>
<td>25 ± 3</td>
<td>8 ± 2</td>
<td>***</td>
</tr>
<tr>
<td>1992</td>
<td>N applied in spring and two defoliation regimes: last cut before measurement in October and in February</td>
<td>32 ± 4</td>
<td>15 ± 2</td>
<td>***</td>
</tr>
<tr>
<td>1995</td>
<td>N applied in spring, last cut before measurement in February</td>
<td>36 ± 8</td>
<td>18 ± 4</td>
<td>***</td>
</tr>
<tr>
<td>1996</td>
<td>N applied in spring, last cut before measurement in October</td>
<td>69 ± 5</td>
<td>30 ± 5</td>
<td>***</td>
</tr>
</tbody>
</table>

*** Significant at $P < 0.001$. 

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Fig. 3. Stem length of reproductive tillers (dotted line) and lamina length on an average tiller (continuous line) over the studied period (degree-days from 1 February) in 1995 and 1996 for treatments with severe defoliation with N application or nil; vertical bars indicate standard error of 1.
was very close to that found on average over a growing period (Fig. 5). We concluded that RUE computed over a growth period, before leaf senescence and stem elongation occurred, was a suitable variable for herbage accumulation modeling.

Given the structure chosen for the model, the parameters needed were leaf life span, amount of matter remobilized during senescence, and increase in RUE over the stem elongation phase. We found that these parameters could vary according to environmental conditions. To determine a value for these parameters, the previous results were compared with those found in the literature.

Because SLA was measured before the complete senescence of the lamina, the losses of lamina mass were underestimated. Moreover, the increase in SLA during senescence resulted both from remobilization (mainly of minerals; Wilman et al., 1994) and respiratory losses. Remobilization up to 30% was observed (Robson and Deacon, 1978). For our model, in which the RUE takes account of losses due to respiration, we chose a remobilization coefficient (λ) of 15%, the average value from the data of Table 5.

Whereas leaf life span was less variable between seasons when expressed in DD, differences remained, e.g., about 200 DD between 1994 and 1995. The optimum temperature for most aspects of cool-season grass leaf growth tends to be in the range of 20 to 25°C (Robson et al., 1988). In our experimental conditions, this temperature was very often exceeded in summer, particularly in 1994. When maximal daily temperature reached 25°C, average daily temperature was around 18°C. Hence, we computed the accumulated temperatures, setting an upper limit to the average daily temperature of 18°C. For treatments with applied N, the leaf life span fell between 770 (1997) and 850 DD (1994). However, this calculation did not explain the earlier senescence pat-
Fig. 5. Radiation use efficiency (RUE) related to herbage N index (Ni) over vegetative phase for lenient defoliation (continuous line; $\text{RUE} = 0.0210\text{Ni} - 0.48, r^2 = 0.89, \text{SE} = 0.11$) and for severe defoliation (dotted line; $\text{RUE} = 0.0190\text{Ni}, r^2 = 0.94, \text{SE} = 0.11$). Pooling the data of both defoliation regimes, we found $\text{RUE} = 0.0195\text{Ni} - 0.0018 \times \text{residual herbage mass}, r^2 = 0.94, \text{SE} = 0.12$.

Model Validation

Measured and simulated herbage DM accumulation over a regrowth period were compared. Input variables were herbage N status, residual herbage mass, temperature, and radiation. Reproductive tiller density was used to analyze discrepancies between measured and simulated herbage mass.

For spring growths at Toulouse, a decrease in herbage mass was observed at the beginning of regrowth in 1990 and in 1992 as mentioned above for 1996. In these cases, simulation began at the second or third measurement date, and $W_2$ was the herbage mass at this date. For the whole data set, we have $\text{RMSE} = 55.7 \text{ g m}^{-2} (n = 93)$. There was a trend to overestimate the standing herbage mass in 1989 and to underestimate it in 1995 and 1996 (Fig. 6). The difference between simulated and observed data was greatest for the highest herbage mass.

During the stem elongation phase (end of April to beginning of May), herbage mass was overestimated in 1989, 1990, and 1992 (data not shown) when the proportion of reproductive tillers was lowest (Table 6) and underestimated in 1995 and 1996. In 1989 and 1992, the smaller proportion of reproductive tillers could be a result of the early spring cut (Table 2) (Gillet, 1980). In other words, the pattern in herbage accumulation rate over the stem elongation period would be better simulated by taking into account the proportion of reproductive tillers than the herbage Ni and temperature (Eq. [10]). For vegetative regrowths, there was a tendency to underestimate the herbage mass (Fig. 6), particularly in 1991 ($\text{RMSE} = 10.7 \text{ g m}^{-2}, n = 80$). This discrepancy was in agreement with slight differences observed between spring and summer regrowths for Severn treatments (Fig. 4).

For the Pyrenean site (Fig. 6), RMSE was an average of 12.0 g m$^{-2}$. However, the accuracy of the prediction was highest for the leafy herbage in early spring ($\text{RMSE} = 16.3 \text{ g m}^{-2}, n = 22$) and for vegetative regrowths following spring grazing ($\text{RMSE} = 18.7 \text{ g m}^{-2}, n = 27$). Conversely, accuracy was lowest at the hay stage, after grass flowering, for plots that were not grazed in spring ($\text{RMSE} = 29.4 \text{ g m}^{-2}, n = 22$). However, it is for this defoliation regime that differences in phenology (flowering times) between orchardgrass and other species could be the greatest, leading to different patterns of growth and senescence and lower accuracy of DM yield predictions.

For the Segala site, we compared the net herbage accumulation between post- and pregrazing times (Fig. 6). The RMSE was higher for other sites (47.2 g m$^{-2}$), but it was for this database that growth duration between two defoliations was shortest (Table 2) and the average herbage accumulated lowest (only 88 g m$^{-2}$). Furthermore, net herbage accumulation could be negative when the residual sward mass was high. There was a trend to underestimate net herbage accumulation over the reproductive period (before the heading stage, 15 May) and to overestimate it later (Fig. 6d). The fact that these weeds were grazed and not pure orchardgrass could be the reason for the lower accuracy of this data set.

GENERAL DISCUSSION AND CONCLUSION

The aim of the model was to simulate net herbage accumulation rate for wide ranges of residual herbage bio-
Fig. 6. Simulated (Y) and measured (X) (i) herbage dry matter at the Toulouse site for orchardgrass spring growth (Y = 0.87X + 31.4, r² = 0.93, SE = 35.6) and summer growth (Y = 0.86X + 2.6, r² = 0.97, SE = 29.4), (ii) herbage dry matter at the Pyrenees site for permanent grasslands (Y = 0.56X + 176, r² = 0.52, SE = 79.5), and (iii) net herbage accumulation between post- and pregrazing times in the Segala site over the reproductive and vegetative phases (Y = 0.66X + 40.8, r² = 0.57, SE = 40.0). Dotted line: Y = X.

Whereas the values of the parameters found for the vegetative regrowths were similar to those obtained previously (Bélanger et al., 1992; Duru et al., 1995), the growth submodel is subject to several limitations. Like Bélanger et al. (1992), we only found a small difference in RUE between summer regrowths and the vegetative phase of spring regrowths. In the literature, RUE was usually found to increase below an optimal temperature and decrease beyond it (Brisson et al., 1998). This means that the effect of lower temperatures in spring (about 5°C at a weekly scale) must be offset by an effect of development stage in spring. According to Brisson et al. (1998), when average daily temperature fell from 20°C (considered optimal for growth of main cool-season
grasses) to 10°C, RUE decreased by 25%. In fact, RUE as well as leaf extension rate can also increase from the double-ridge stage for a vernalized tiller as a result of less assimilate being directed towards roots (Bélanger et al., 1994) and of a sward structure more favorable for photosynthetic activity, even before stem elongation (Parsons, 1988). This last point is probably due to the distance of the lamina from different insertion levels on the sheath, which was greater in spring than in summer (Duru and Ducrocq, 2000). Residual biomass led to lower net herbage accumulation rate, both through leaf losses and leaf respiration. We only explicitly take into account the first process. High herbage mass increased leaf respiration without increasing photosynthesis rate (Parsons, 1988). We did not attempt to model this process, which was empirically taken into account in the RUE parameters.

The senescence submodel takes into account a large amount of residual biomass. However, at the end of winter, tiller mortality also had an effect on the standing herbage mass, increasing the normal death rate due to leaf life span. We are not yet able to define the circumstances that led to tiller mortality, with a view to taking it into account in a sink-driven model. The model could readily be adapted to other grass species and environmental conditions. Previously, the same model structure was used to compare growth of orchardgrass and tall fescue (Festuca arundinacea Schreb.) during the vegetative phase before herbage senescence occurred (Duru et al., 1995). We have shown here that such a model could be improved by including the senescence submodel, taking into account differences in leaf life span and plant phenology. For the spring period, further studies should be done to clarify the effects of defoliation regimes (grazing date and pressure) on the proportion of reproductive vs. vegetative tillers. A water balance module, based on evaporation from the soil and maximal transpiration, as is commonly used in growth models (Brisson et al., 1998; Schapendonk et al., 1998), could be added to simulate the effects of moisture stress. The main limitation of the model is that there is no soil–plant N submodule to predict the N availability from soil characteristics, animal excretion, and fertilizer application. Unfortunately, better understanding of the processes involved in the supply of N from organic matter is needed to build a prediction model (Jarvis, 1998). In fact, the patterns of N mineralization and immobilization in soils result largely from management practices, which need to be better understood for modeling.

The objective of this research was not to achieve the best prediction of herbage DM as for research model. It was to achieve a simple model, running as a spreadsheet, and to inform advisory services and farmers about the likely effects of different grassland management scenarios on DM yield over a growing season so that these scenarios will be soundly based. We considered, on the basis of validation performed, that this aim was reached.

ACKNOWLEDGMENTS

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