Model Analysis for Partitioning of Dry Matter and Plant Nitrogen for Stem and Leaf in Alfalfa

A. R. Overman and R. V. Scholtz III
Agricultural and Biological Engineering Department, University of Florida, Gainesville, Florida, USA

Abstract: The expanded growth model was developed to describe accumulation of dry matter and plant nutrients with time for annual and perennial crops. It incorporates an environmental driving function and an intrinsic growth function. Previous analysis has shown that the model applies to the annual corn (Zea mays L.) and the warm season perennial bermudagrass (Cynodon dactylon L. Pers.). In this article, the model is used to describe accumulation of dry matter and plant nitrogen by alfalfa (Medicago sativa L.). Data confirm the hyperbolic phase relationship between plant N and dry matter for the whole plant. Further analysis confirms a linear relationship between leaf and stem dry matter. The model is used to simulate growth of stems with time, and a linear equation then used to link leaf and stem mass. Stem and leaf N are then related to stem and leaf dry matter through hyperbolic equations.

Keywords: Models, nutrients, forage grass

INTRODUCTION

The expanded growth model for plant accumulation of dry matter and nutrients is the culmination of 20 years of effort. Our first step was the empirical model applied to perennial grasses (Overman 1984; Overman, Angley, and Wilkinson 1998a, 1998b; Overman, Wilson, and Vidak 1995).
This was followed by a phenomenological model (Overman, Angley, and Wilkinson 1989; Overman, Angley, and Wilkinson 1990), which incorporated a Gaussian environmental function and a linear intrinsic growth function. It worked for perennial grasses up to harvest intervals of 6 weeks, but it did not work for annuals. The intrinsic growth function was then modified to a linear-exponential form to develop the expanded growth model (Overman 1998), which was shown to apply to annuals and perennials (Overman and Wilson 1999). A mathematical theorem was subsequently proven, which established linear-exponential dependence of seasonal dry matter on harvest interval for perennials harvested on a fixed time interval (Overman 2001).

This article discusses application of the expanded growth model to data for alfalfa, including partitioning of dry matter and plant N between stems and leaves. Detailed procedures are provided to illustrate application of the model.

MODEL DESCRIPTION

The expanded growth model has been discussed in detail previously (Overman 1998). It consists of two components: 1) an environmental driving function and 2) an intrinsic growth function. The Gaussian environmental function, \( E \), is given by

\[
E = \text{constant} \cdot \exp\left[ -\left( \frac{t - \mu}{\sqrt{2\sigma}} \right)^2 \right] \tag{1}
\]

where \( t \) is calendar time from January 1, wk; \( \mu \) is time to the mean of the distribution, wk; and \( \sigma \) is time spread of the distribution, wk. The intrinsic growth function is assumed to follow the linear-exponential form

\[
\frac{dY'}{dt} = [a + b(t - t_i)] \exp[-c(t - t_i)] \tag{2}
\]

where \( dY'/dt \) is rate of accumulation of dry matter under constant environmental conditions, Mg ha\(^{-1}\) wk\(^{-1}\); \( a \) is initial growth rate at \( t = t_i \), Mg ha\(^{-1}\) wk\(^{-1}\); \( b \) is coefficient of increase in growth rate, Mg ha\(^{-1}\) wk\(^{-2}\); \( c \) is coefficient of aging, wk\(^{-1}\); and \( t_i \) is time of initiation of growth, wk. Net growth rate, \( dY/dt \), is taken as the product of Eqs. (1) and (2), so that

\[
\frac{dY}{dt} = \text{constant} \cdot [a + b(t - t_i)] \exp[-(t - t_i)] \exp\left[ -\left( \frac{t - \mu}{\sqrt{2\sigma}} \right)^2 \right] \tag{3}
\]

It should be noted that Eq. (3) contains two reference times (i.e., \( t_i \) and \( \mu \)) related to the plant and environment, respectively. Overman (1998) showed that Eq. (3) could be integrated to obtain the linear yield function

\[
Y = AQ \tag{4}
\]
where $Y$ is dry matter, Mg ha$^{-1}$; $A$ is yield factor, Mg ha$^{-1}$; and $Q$ is growth quantifier defined by

$$Q = \exp\left(\sqrt{2}\sigma cx_i\right)$$

$$\times \left\{ (1 - kx_i)[\text{erf} x - \text{erf} x_i] - \frac{k}{\sqrt{\pi}}[\exp(-x^2) - \exp(-x_i^2)] \right\}$$

(5)

where $k$ is dimensionless curvature factor in the intrinsic growth function, defined by

$$k = \frac{\sqrt{2}\sigma b}{a}$$

(6)

and $x$ is dimensionless time variable defined by

$$x = \frac{t - \mu}{\sqrt{2}\sigma} + \frac{\sqrt{2}\sigma c}{2}$$

(7)

where $x_i$ is dimensionless time corresponding to the time of initiation of growth, $t_i$. The error function in Eq. (5) is defined by

$$\text{erf} x = \frac{2}{\sqrt{\pi}} \int_0^x \exp(-u^2)du$$

(8)

where $u$ is simply the variable of integration. Values for the error function can be obtained from mathematical tables (Abramowitz and Stegun 1965).

Based on examination of data, plant N accumulation is assumed to be related to dry matter accumulation through the hyperbolic relationship

$$N_u = \frac{N_{um}Y}{K_y + Y}$$

(9)

where $N_u$ is plant N accumulation, kg ha$^{-1}$; $N_{um}$ is potential maximum plant N accumulation, kg ha$^{-1}$; and $K_y$ is yield response coefficient, Mg ha$^{-1}$. Equation (9) can be rearranged to the linear form

$$\frac{Y}{N_u} = \frac{K_y}{N_{um}} + \frac{1}{N_{um}} Y$$

(10)

Equations (9) and (10) constitute the phase relationships for the model. Plant N concentration, $N_c$, can be derived from Eq. (9)

$$N_c = \frac{N_u}{Y} = \frac{N_{um}}{K_y + Y}$$

(11)
DATA ANALYSIS

Data for this analysis are taken from a study with alfalfa (cv. Vernal) at Guelph, Ontario, Canada, by Fulkerson (1983). Plant samples were collected at different stages of growth beginning on May 22. Results for dry matter and plant N for the whole plant (above ground) are given in Table 1 and shown in Figures 1 and 2.

From the graph of $Y$ vs. $t$, the time of initiation is selected to be $t_i = 17.5$ wk. From previous experience with the model (Overman 1998; Overman and Wilson 1999), parameters are chosen as $\mu = 26$ wk, $\sqrt{2\sigma} = 8$ wk, $c = 0.30$ wk$^{-1}$, $k = 5$. Substitution of these values into Eq. (7) leads to

$$x = \frac{t - 26}{8} + 1.20 = \frac{t - 16.4}{8}, \quad x_i = 0.1375 \quad (12)$$

The equation for the growth quantifier now becomes

$$Q = 1.391\left[0.312[\text{erf} - 0.115] - 2.821[\exp(-x^2) - 0.981]\right] \quad (13)$$

Estimates for the growth model are compiled in Table 2. Values of $Y = 5.00$ Mg ha$^{-1}$ and $Q = 2.545$ at $t = 24$ wk are chosen from Figure 1 to calibrate the model

$$Y = AQ = \left(\frac{5.00}{2.545}\right)Q = 1.96Q \quad (14)$$

Equation 14 are used to obtain yield estimates in Table 2.

Table 1. Growth response of dry matter ($Y$), plant N concentration ($N_c$), and plant N uptake ($N_u$) with calendar time ($i$) for alfalfa grown at Guelph, Ontario, Canada$^a$

<table>
<thead>
<tr>
<th>$t$ wk</th>
<th>$Y$ Mg ha$^{-1}$</th>
<th>$N_c$ g kg$^{-1}$</th>
<th>$N_u$ kg ha$^{-1}$</th>
<th>$Y/N_u$ kg g$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>20.3</td>
<td>1.75</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>21.1</td>
<td>2.74</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>22.1</td>
<td>3.40</td>
<td>36.5</td>
<td>124</td>
<td>0.0274</td>
</tr>
<tr>
<td>23.1</td>
<td>4.45</td>
<td>32.4</td>
<td>144</td>
<td>0.0309</td>
</tr>
<tr>
<td>24.1</td>
<td>5.15</td>
<td>29.7</td>
<td>153</td>
<td>0.0337</td>
</tr>
<tr>
<td>25.1</td>
<td>5.90</td>
<td>27.3</td>
<td>160</td>
<td>0.0366</td>
</tr>
<tr>
<td>26.3</td>
<td>6.38</td>
<td>25.2</td>
<td>162</td>
<td>0.0397</td>
</tr>
<tr>
<td>27.1</td>
<td>7.12</td>
<td>24.0</td>
<td>171</td>
<td>0.0417</td>
</tr>
<tr>
<td>28.1</td>
<td>7.23</td>
<td>22.4</td>
<td>162</td>
<td>0.0466</td>
</tr>
<tr>
<td>29.1</td>
<td>6.82</td>
<td>22.1</td>
<td>151</td>
<td>0.0452</td>
</tr>
</tbody>
</table>

$^a$Data adapted from Fulkerson (1983). Calendar time is referenced to January 1.
Phase plots are shown in Figure 2 for the whole plant. The straight line is drawn from

\[
\frac{Y}{N_u} = 0.0121 + 0.00428Y, \quad r = 0.9896
\]  

**Figure 1.** Growth response of dry matter (\(Y\)), plant N uptake (\(N_u\)), and plant N concentration (\(N_c\)) for alfalfa grown at Guelph, Ontario, Canada. Data adapted from Fulkerson (1983). Curves drawn from Eqs. (12)–(14), (16), and (17).
Figure 2. Phase plot ($N_u$ and $Y/N_u$ vs. $Y$) for alfalfa grown at Guelph, Ontario, Canada. Data adapted from Fulkerson (1983). Line drawn from Eq. (15); curve drawn from Eq. (16).

for $22.1 \leq t \leq 28.1$ wk. This leads to the hyperbolic equations

$$
\hat{N}_u = \frac{234Y}{2.83 + Y} \tag{16}
$$

$$
\hat{N}_e = \frac{234}{2.83 + Y} \tag{17}
$$

Equation (16) is used to draw the curve in Figure 2. Yield estimates from Table 2 are substituted into Eqs. (16) and (17) to calculate plant N uptake and
plant N concentration, which are then used to draw the middle and top curves in Figure 1.

Data for alfalfa dry matter and plant N for stem and leaf fractions are given in Table 3. The challenge is to develop a simulation procedure for the

Table 2. Model estimates of dry matter and plant N with time for alfalfa grown at Guelph, Ontario, Canada

<table>
<thead>
<tr>
<th>t, wk</th>
<th>x</th>
<th>erf, x</th>
<th>exp((-x^2))</th>
<th>Q</th>
<th>(\hat{Y} ), Mg ha(^{-1})</th>
<th>(\hat{N}_u, ) kg ha(^{-1})</th>
<th>(\hat{N}_c, ) g kg(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>17.5</td>
<td>0.138</td>
<td>0.155</td>
<td>0.981</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>82.7</td>
</tr>
<tr>
<td>18</td>
<td>0.200</td>
<td>0.223</td>
<td>0.961</td>
<td>0.108</td>
<td>0.21</td>
<td>16.2</td>
<td>77.1</td>
</tr>
<tr>
<td>19</td>
<td>0.325</td>
<td>0.354</td>
<td>0.900</td>
<td>0.404</td>
<td>0.79</td>
<td>51.6</td>
<td>64.5</td>
</tr>
<tr>
<td>20</td>
<td>0.450</td>
<td>0.475</td>
<td>0.817</td>
<td>0.782</td>
<td>1.53</td>
<td>82.5</td>
<td>53.6</td>
</tr>
<tr>
<td>21</td>
<td>0.575</td>
<td>0.584</td>
<td>0.718</td>
<td>1.218</td>
<td>2.39</td>
<td>107</td>
<td>44.6</td>
</tr>
<tr>
<td>22</td>
<td>0.700</td>
<td>0.678</td>
<td>0.613</td>
<td>1.671</td>
<td>3.28</td>
<td>126</td>
<td>38.3</td>
</tr>
<tr>
<td>23</td>
<td>0.825</td>
<td>0.757</td>
<td>0.506</td>
<td>2.125</td>
<td>4.16</td>
<td>140</td>
<td>33.5</td>
</tr>
<tr>
<td>24</td>
<td>0.950</td>
<td>0.821</td>
<td>0.406</td>
<td>2.545</td>
<td>5.00</td>
<td>150</td>
<td>29.9</td>
</tr>
<tr>
<td>25</td>
<td>1.075</td>
<td>0.872</td>
<td>0.315</td>
<td>2.925</td>
<td>5.73</td>
<td>157</td>
<td>27.3</td>
</tr>
<tr>
<td>26</td>
<td>1.200</td>
<td>0.910</td>
<td>0.237</td>
<td>3.247</td>
<td>6.36</td>
<td>162</td>
<td>25.4</td>
</tr>
<tr>
<td>27</td>
<td>1.325</td>
<td>0.939</td>
<td>0.173</td>
<td>3.511</td>
<td>6.88</td>
<td>166</td>
<td>24.0</td>
</tr>
<tr>
<td>28</td>
<td>1.450</td>
<td>0.960</td>
<td>0.122</td>
<td>3.716</td>
<td>7.28</td>
<td>169</td>
<td>23.1</td>
</tr>
<tr>
<td>29</td>
<td>1.575</td>
<td>0.974</td>
<td>0.0837</td>
<td>3.876</td>
<td>7.60</td>
<td>171</td>
<td>22.4</td>
</tr>
<tr>
<td>30</td>
<td>1.700</td>
<td>0.984</td>
<td>0.0556</td>
<td>3.992</td>
<td>7.82</td>
<td>172</td>
<td>21.9</td>
</tr>
</tbody>
</table>

Data adapted from Fulkerson (1983). Calendar time is referenced to January 1.

Table 3. Growth response of dry matter (\(Y\)), plant N concentration (\(N_c\)), and plant N uptake (\(N_u\)) with calendar time (\(t\)) for alfalfa leaves and stems growth at Guelph, Ontario, Canada\(^a\)

<table>
<thead>
<tr>
<th>t, wk</th>
<th>(Y), Mg ha(^{-1})</th>
<th>(N_c), g kg(^{-1})</th>
<th>(N_u), kg ha(^{-1})</th>
<th>(Y/N_u), kg g(^{-1})</th>
<th>(Y), Mg ha(^{-1})</th>
<th>(N_c), g kg(^{-1})</th>
<th>(N_u), kg ha(^{-1})</th>
<th>(Y/N_u), kg g(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>20.3</td>
<td>1.14 — — — —</td>
<td>0.61 — — — —</td>
<td>0.61 — — — —</td>
<td>0.61 — — — —</td>
<td>0.61 — — — —</td>
<td>0.61 — — — —</td>
<td>0.61 — — — —</td>
<td>0.61 — — — —</td>
</tr>
<tr>
<td>22.1</td>
<td>1.67 50.9 85.0 0.0196</td>
<td>1.73 22.4 38.8 0.0446</td>
<td>1.73 22.4 38.8 0.0446</td>
<td>1.73 22.4 38.8 0.0446</td>
<td>1.73 22.4 38.8 0.0446</td>
<td>1.73 22.4 38.8 0.0446</td>
<td>1.73 22.4 38.8 0.0446</td>
<td>1.73 22.4 38.8 0.0446</td>
</tr>
<tr>
<td>23.1</td>
<td>2.02 48.5 98.0 0.0260</td>
<td>2.43 19.0 46.2 0.0526</td>
<td>2.43 19.0 46.2 0.0526</td>
<td>2.43 19.0 46.2 0.0526</td>
<td>2.43 19.0 46.2 0.0526</td>
<td>2.43 19.0 46.2 0.0526</td>
<td>2.43 19.0 46.2 0.0526</td>
<td>2.43 19.0 46.2 0.0526</td>
</tr>
<tr>
<td>24.1</td>
<td>2.22 46.6 103 0.0215</td>
<td>2.93 17.0 49.8 0.0588</td>
<td>2.93 17.0 49.8 0.0588</td>
<td>2.93 17.0 49.8 0.0588</td>
<td>2.93 17.0 49.8 0.0588</td>
<td>2.93 17.0 49.8 0.0588</td>
<td>2.93 17.0 49.8 0.0588</td>
<td>2.93 17.0 49.8 0.0588</td>
</tr>
<tr>
<td>25.1</td>
<td>2.44 43.5 106 0.0230</td>
<td>3.46 15.7 54.3 0.0637</td>
<td>3.46 15.7 54.3 0.0637</td>
<td>3.46 15.7 54.3 0.0637</td>
<td>3.46 15.7 54.3 0.0637</td>
<td>3.46 15.7 54.3 0.0637</td>
<td>3.46 15.7 54.3 0.0637</td>
<td>3.46 15.7 54.3 0.0637</td>
</tr>
<tr>
<td>26.3</td>
<td>2.49 41.6 104 0.0240</td>
<td>3.89 14.9 58.0 0.0671</td>
<td>3.89 14.9 58.0 0.0671</td>
<td>3.89 14.9 58.0 0.0671</td>
<td>3.89 14.9 58.0 0.0671</td>
<td>3.89 14.9 58.0 0.0671</td>
<td>3.89 14.9 58.0 0.0671</td>
<td>3.89 14.9 58.0 0.0671</td>
</tr>
<tr>
<td>27.1</td>
<td>2.72 39.2 107 0.0255</td>
<td>4.40 14.6 64.2 0.0685</td>
<td>4.40 14.6 64.2 0.0685</td>
<td>4.40 14.6 64.2 0.0685</td>
<td>4.40 14.6 64.2 0.0685</td>
<td>4.40 14.6 64.2 0.0685</td>
<td>4.40 14.6 64.2 0.0685</td>
<td>4.40 14.6 64.2 0.0685</td>
</tr>
<tr>
<td>28.1</td>
<td>2.36 38.4 90.6 0.0260</td>
<td>4.87 14.7 71.6 0.0680</td>
<td>4.87 14.7 71.6 0.0680</td>
<td>4.87 14.7 71.6 0.0680</td>
<td>4.87 14.7 71.6 0.0680</td>
<td>4.87 14.7 71.6 0.0680</td>
<td>4.87 14.7 71.6 0.0680</td>
<td>4.87 14.7 71.6 0.0680</td>
</tr>
<tr>
<td>29.1</td>
<td>2.14 37.0 79.2 0.0270</td>
<td>4.68 15.4 72.1 0.0649</td>
<td>4.68 15.4 72.1 0.0649</td>
<td>4.68 15.4 72.1 0.0649</td>
<td>4.68 15.4 72.1 0.0649</td>
<td>4.68 15.4 72.1 0.0649</td>
<td>4.68 15.4 72.1 0.0649</td>
<td>4.68 15.4 72.1 0.0649</td>
</tr>
</tbody>
</table>

\(^a\)Data adapted from Fulkerson (1983). Calendar time is referenced to January 1.
two plant fractions. A phase plot of dry matter for leaves \((Y_l)\) vs. stems \((Y_s)\) is shown in Figure 3. The trend appears to be linear, which leads to
\[
\hat{Y}_l = a + bY_s = 1.037 + 0.390Y_s, \quad r = 0.9867 \tag{18}
\]
where \(a\) and \(b\) are intercept and slope parameters, respectively. Values at \(t = 28.1\) and 29.1 wk have been omitted from regression analysis. The leaf fraction \((f_l)\) is defined by
\[
\hat{f}_l = \frac{\hat{Y}_l}{Y_l + Y_s} = \frac{a + b\hat{Y}_s}{a + (b + 1)\hat{Y}_s} = \frac{1.037 + 0.390\hat{Y}_s}{1.037 + 1.390\hat{Y}_s} \tag{19}
\]
which is also shown in Figure 3. Note that time is implicit in the plots. The linear phase relation is consistent with recent analysis of partitioning of leaves and stems in bermudagrass (Overman and Scholtz 2004).
The choice is now made to simulate growth of stems with time. Parameters are chosen as $t_i = 18.5$ wk, $\mu = 26$ wk, $\sqrt{2\sigma} = 8$ wk, $c = 0.30$ wk$^{-1}$, and $k = 5$. Substitution of these values into Eq. (7) leads to

$$x = \frac{t - 26}{8} + 1.20 = \frac{t - 16.4}{8}, \quad x_i = 0.2625$$  \hspace{1cm} (20)

The equation for the growth quantifier becomes

$$Q = 1.878 [-0.312 \text{erf} x - 0.290] - 2.821 \exp(-x^2) - 0.933]$$  \hspace{1cm} (21)

Estimates for the growth model for stems are compiled in Table 4. Values of $Y_s = 3.80$ Mg ha$^{-1}$ and $Q = 3.324$ at $t = 26$ wk are used to calibrate the model

$$\hat{Y}_s = AQ = \left( \frac{3.80}{3.324} \right) Q = 1.143Q$$  \hspace{1cm} (22)

Equation (22) is used to obtain yield estimates for stems in Table 4. Phase plots to relate plant N and dry matter accumulation for stems and leaves are shown in Figure 4, where the lines and curves are drawn from

Stems:

$$\frac{Y_s}{N_{us}} = \frac{K_s}{N_{ums}} + \frac{1}{N_{ums}} Y_s = 0.0269 + 0.0105Y_s, \quad r = 0.9968$$  \hspace{1cm} (23)

<table>
<thead>
<tr>
<th>$t$, wk</th>
<th>$x$</th>
<th>erf, $x$</th>
<th>exp$(-x^2)$</th>
<th>$Q$</th>
<th>$\hat{Y}_s$, Mg ha$^{-1}$</th>
<th>$\hat{N}_{ur}$, kg ha$^{-1}$</th>
<th>$\hat{N}_{cr}$, g kg$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>18.5</td>
<td>0.262</td>
<td>0.290</td>
<td>0.933</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>37.2</td>
</tr>
<tr>
<td>19</td>
<td>0.325</td>
<td>0.354</td>
<td>0.900</td>
<td>0.137</td>
<td>0.16</td>
<td>5.5</td>
<td>35.0</td>
</tr>
<tr>
<td>20</td>
<td>0.450</td>
<td>0.475</td>
<td>0.817</td>
<td>0.506</td>
<td>0.59</td>
<td>17.8</td>
<td>30.2</td>
</tr>
<tr>
<td>21</td>
<td>0.575</td>
<td>0.584</td>
<td>0.718</td>
<td>0.967</td>
<td>1.11</td>
<td>28.8</td>
<td>25.9</td>
</tr>
<tr>
<td>22</td>
<td>0.700</td>
<td>0.678</td>
<td>0.613</td>
<td>1.468</td>
<td>1.68</td>
<td>37.7</td>
<td>22.4</td>
</tr>
<tr>
<td>23</td>
<td>0.825</td>
<td>0.757</td>
<td>0.506</td>
<td>1.989</td>
<td>2.28</td>
<td>44.8</td>
<td>19.6</td>
</tr>
<tr>
<td>24</td>
<td>0.950</td>
<td>0.821</td>
<td>0.406</td>
<td>2.481</td>
<td>2.84</td>
<td>50.0</td>
<td>17.6</td>
</tr>
<tr>
<td>25</td>
<td>1.075</td>
<td>0.872</td>
<td>0.315</td>
<td>2.933</td>
<td>3.36</td>
<td>53.9</td>
<td>16.0</td>
</tr>
<tr>
<td>26</td>
<td>1.200</td>
<td>0.910</td>
<td>0.237</td>
<td>3.324</td>
<td>3.80</td>
<td>56.7</td>
<td>14.9</td>
</tr>
<tr>
<td>27</td>
<td>1.325</td>
<td>0.939</td>
<td>0.173</td>
<td>3.646</td>
<td>4.17</td>
<td>58.8</td>
<td>14.1</td>
</tr>
<tr>
<td>28</td>
<td>1.450</td>
<td>0.960</td>
<td>0.122</td>
<td>3.903</td>
<td>4.46</td>
<td>60.3</td>
<td>13.5</td>
</tr>
<tr>
<td>29</td>
<td>1.575</td>
<td>0.974</td>
<td>0.0837</td>
<td>4.099</td>
<td>4.69</td>
<td>61.4</td>
<td>13.1</td>
</tr>
<tr>
<td>30</td>
<td>1.700</td>
<td>0.984</td>
<td>0.0556</td>
<td>4.242</td>
<td>4.85</td>
<td>62.1</td>
<td>12.8</td>
</tr>
</tbody>
</table>
Figure 4. Phase plot ($N_u$ and $Y/N_u$ vs. $Y$) for stems and leaves for alfalfa grown at Guelph, Ontario, Canada. Data adapted from Fulkerson (1983). Lines drawn from Eqs. (23) and (26); curves drawn from Eqs. (24) and (27).

\[
N_{us} = \frac{N_{ums}Y_s}{K_s + Y_s} = \frac{95.2Y_s}{2.56 + Y_s} \tag{24}
\]

\[
N_{cs} = \frac{N_{us}}{Y_s} = \frac{95.2}{2.56 + Y_s} \tag{25}
\]

Leaves:

\[
Y_l = \frac{K_l}{N_{uml}} + \frac{1}{N_{uml}}Y_l = 0.00946 + 0.00571Y_l, \quad r = 0.9700 \tag{26}
\]

\[
N_{ul} = \frac{N_{uml}Y_l}{K_l + Y_l} = \frac{175Y_l}{1.66 + Y_l} \tag{27}
\]

\[
N_{cl} = \frac{N_{ul}}{Y_l} = \frac{175}{1.66 + Y_l} \tag{28}
\]
For regression purposes, the last three points are omitted for stems and the last two for leaves, due to shedding of leaves toward the end of the growth period. Simulation curves for stems and leaves are shown in Figure 5, where estimates of variables are made from Eqs. (18), (24), (25), (27), and (28).

Figure 5. Growth response of dry matter ($Y$), plant N uptake ($N_u$), and plant N concentration ($N_c$) for alfalfa leaves and stems grown at Guelph, Ontario, Canada. Data adapted from Fulkerson (1983). Curves drawn from Eqs. (20)–(22), (24), (25), (27), and (28).
SUMMARY AND CONCLUSIONS

Several conclusions can be drawn from this analysis. First, the expanded growth model provides excellent description of accumulation of dry matter and plant N with time for the whole plant (Figure 1). The phase plot between plant N uptake and dry matter follows a hyperbolic relationship (Figure 2). For many field experiments, this will be the extent of the data.

Second, in the case of data for partitioning between stems and leaves, a choice must be made between either simulation of each component or simulation of one component and some relationship between the two components. The latter was chosen with a linear phase relationship [Eq. (18)] between leaves and stems (Figure 3) and simulation of stem accumulation with time [Eqs. (20)–(22)]. These results suggest that the rate-limiting process is formation of stem mass and that leaf and stem mass develop in virtual equilibrium after the initial flush of leaf development. Now Eq. (18) does not mean that stem growth causes leaf growth, but that there is linkage between the two. Further analysis of this point is definitely needed. It is assumed that linkage between plant N uptake and dry matter is hyperbolic for both stem and leaf components (Figure 4). This allows full simulation of dry matter and plant N accumulation with time for both stems and leaves (Figure 5).

For the purpose of estimating crop yields and plant N accumulation, the use of Eqs. (12)–(17) is suggested, as shown in Figures 1 and 2. This approach has proven useful for several crops and field conditions (Overman and Scholtz 2002). It is what might be referred to as an effective model (Krauss 1993), which focuses on relevant factors and ignores those deemed irrelevant for the model. An alternative would be to model the vertical distribution of dry matter (Overman and Wilkinson 1991; Overman 2002). The analysis on partitioning is included to provide insight into the detailed processes inherent in crop growth (Figures 3–5).

Finally, a word about philosophy of method: the Greek approach and the Babylonian approach. The Greek approach follows from first principles and axioms, whereas the Babylonian approach simply relates one thing to another (Mehra 1994). Richard Feynman considered himself a Babylonian. The approach to modeling in this article falls into this category as well. Ideas and concepts embodied in the mathematical models have been verified in the tradition of physics (Segrè 1980).

REFERENCES

Fulkerson, R.S. (1983) Research Review of Forage Production; Crop Science Department, University of Guelph: Ontario, Canada.


