

# Vegetative crop growth model incorporating leaf area expansion and senescence, and applied to grass

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**Abstract.** A crop growth model incorporating leaf area expansion and senescence is constructed. Leaf area is treated as an independent state variable with the incremental specific leaf area a function of the storage/structure ratio. The vegetative grass crop, which usually has three green leaves per tiller, is particularly considered; the above-ground dry matter is assumed to occupy four compartments: growing leaves, first fully expanded leaves, second fully expanded leaves, and senescent leaves. Each compartment is described by two state variables—structural weight and leaf area index. Newly synthesized structural material comprises leaf, sheath and stem in fixed proportions, although defoliation can alter these proportions in the standing crop. Photosynthesis and respiration are calculated in the usual way. Root growth, root: shoot partitioning, soil water and nutrients are assumed to be relatively unimportant for an established vegetative grass crop grown under favourable conditions. The model is used to simulate the time course of dry matter and leaf area development for crops that are exposed to a constant environment, a seasonally varying environment, and are defoliated.

**Key-words:** model; crop growth; grass crop; leaf area; senescence.

## Introduction

Mechanistic models of crop growth provide a means by which knowledge of individual plant and crop processes may be systematically brought together to increase our understanding of the integrated system, and also ultimately to give a valuable predictive tool. Many crop models have already been reported (for example, de Wit *et al.*, 1978; Acock, Charles-Edwards & Sawyer, 1979; Fisher, Charles-Edwards & Campbell, 1980; Sheehy, Cobby & Ryle, 1980; Johnson, Ameziane & Thornley, 1983), and Legg (1981) has written a comprehensive review of some of these and of several other crop models. Mechanistic crop models inevitably consist of sub-models, and one of the more crucial sub-models is concerned with leaf area expansion. However, this area has proved difficult, and there is no consensus about which approaches are biologically plausible and compatible with modelling objectives. A principal feature of the grass growth model described

below is a new approach to the problem of leaf area expansion, which is linked to our treatment of the age structure of the crop, and senescence. As a result, the model is particularly suitable for considering the seasonal effects of grazing and cutting treatments on growth and production, in contrast to the earlier model of Johnson *et al.* (1983), which ignores sward age structure, and where the approach is more appropriate for short-term analytical consideration of the system, unperturbed by grazing or cutting.

There is some agreement amongst crop modellers about methods of calculating light interception and photosynthesis (for example, see Thornley, 1976, chapters 3 and 4), and the traditional approaches are followed here. Similarly with respiration, the basic principles are widely accepted (McCree, 1970, 1982; Thornley, 1970, 1977; Penning de Vries, 1974, 1975; Barnes & Hole, 1978), although there are still some difficulties in allowing for variable maintenance respiratory costs as plants age. In the present grass model, different maintenance coefficients are ascribed to different age categories of plant material. Partitioning and water relations are ignored, since they are unlikely to be of primary consequence for an established vegetative grass crop growing under the conditions considered here—of adequate supply of nutrients and water.

The grass crop is characterized by its ability to adapt to a wide range of conditions, both climatic and imposed by management, as with cutting and grazing. This ability is at least partly due to the plasticity of leaf area expansion, the rapid turnover of material and senescence. A principal aim of this investigation is to construct a model that takes realistic account of these processes, and that may be valuable in the longer term for examining the effects of cutting and grazing regimes on forage crop productivity.

It has often been assumed that leaf area index (LAI) is a *dependent* variable, which can be calculated from the dry weight of the crop and its components. For example, Charles-Edwards & Acock [1977, equation (1)] assumed  $LAI = aW + b$ , where  $W$  is the above-ground dry weight,  $a$  and  $b$  are constants; note that LAI depends only on total dry weight and not on its composition. Both Acock *et al.* (1979, pp. 291–292) and Sheehy *et al.* [1980, equation (11)] assume that the specific leaf area of new leaf tissue (SLA) is an empirical function of temperature

*T* and daily light receipt *J*. Acock *et al.* (1979) take  $\text{SLA} = a + b \ln(T + c/\ln J)$ , and Sheehy *et al.* (1980) take  $\text{SLA} = (a + bT) \exp(-cJ)$ , where *a*, *b* and *c* are constants; in the second expression *T* and *J* take the values of temperature and light received on the day of leaf emergence. Thornley & Hurd [1974, equation (2)] and Johnson *et al.* [1983, equation (3)] assume  $\text{LAI} = aW_G$ , where  $W_G$  is the structural dry weight and *a* is a constant. It is clear that these approaches have limitations; for example, a grass crop which is maintained at a particular LAI value through grazing will be different in structure to a crop which has been cut to that LAI. Also, the environment may fluctuate widely from day to day, so that relating specific leaf area directly to environment may cause physiologically unrealistic variation.

Consequently, in order to overcome these difficulties, leaf area index is treated as an independent state variable. The production of new leaf area is influenced by the level of an assumed storage pool, which also acts as a buffer against environmental fluctuations.

### The model

The scheme assumed is shown in Fig. 1. Symbols are listed in the Appendix. The grass crop is distinguished from other crops by its rapid turnover of leaves. On average there are three live fully expanded leaves per tiller; during the summer the rate of leaf appearance, and therefore loss, is in the region of one leaf per tiller per 10 d (Robson, 1973; Davies, 1977). It is therefore convenient to divide the total above-ground structural crop weight into four categories corresponding to growing leaves, first fully expanded leaves, second fully expanded leaves, and senescing leaves, with structural weights  $W_1$ ,  $W_2$ ,  $W_3$ ,  $W_4$ . There is a single storage component,  $W_S$ ,

supplied by photosynthesis and which is utilized for new structural growth and maintenance. The total structural weight  $W_G$  is

$$W_G = W_1 + W_2 + W_3 + W_4, \quad (1)$$

and the total crop weight is

$$W = W_G + W_S. \quad (2)$$

All components of weight have units  $\text{kg carbon m}^{-2}$ .

The contribution to the LAI of each structural component is  $L_1$ ,  $L_2$ ,  $L_3$ ,  $L_4$ , respectively, and the total LAI is

$$L = L_1 + L_2 + L_3 + L_4. \quad (3)$$

### Light interception and photosynthesis

For light attenuation through the canopy, Beer's Law (Monsi & Saeki, 1953) gives

$$I = I_0 \exp(-kL), \quad (4)$$

where  $I_0$  and  $I$  have units  $\text{J m}^{-2} \text{ s}^{-1}$  photosynthetically active radiation (PAR), and are the light flux densities on a horizontal plane above the canopy and within the canopy at cumulative leaf area index  $L$  respectively;  $k$  is the extinction coefficient. The light flux density incident on the surface of a leaf at depth  $L$ ,  $I_1$ , is (Saeki, 1963)

$$I_1 = \frac{k}{1-\tau} I = \frac{k}{1-\tau} I_0 \exp(-kL), \quad (5)$$

where  $\tau$  is the leaf transmission coefficient.

The gross photosynthetic rate of a leaf,  $P_g$ , is conveniently described by a rectangular hyperbola:

$$P_g = \frac{\alpha I_1 P_m}{\alpha I_1 + P_m}, \quad (6)$$

in units  $\text{kg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .  $\alpha$  is the photosynthetic efficiency ( $\text{kg CO}_2 \text{ J}^{-1}$ ), and  $P_m$  is the limiting value

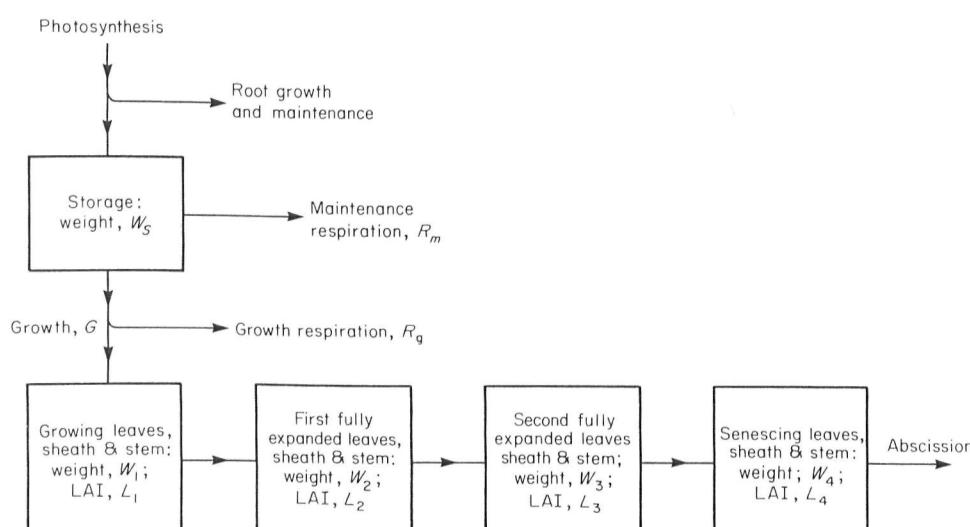


Figure 1. Schematic representation of the model. LAI denotes leaf area index. The crop weights are in carbon units.

of  $P_g$  as  $I_1 \rightarrow \infty$ . The canopy gross photosynthetic rate,  $P_c$ , is obtained by combining equations (5) and (6) and integrating through the canopy to give

$$P_c = \frac{P_m}{k} \ln \left[ \frac{\alpha k I_0 + (1-\tau) P_m}{\alpha k I_0 \exp(-kL) + (1-\tau) P_m} \right], \quad (7)$$

with units  $\text{kg CO}_2 (\text{m}^2 \text{ of ground})^{-1} \text{ s}^{-1}$ . A single value of  $P_m$  is ascribed to the four compartments, which only depends here on temperature. Thus it is assumed that  $P_m$  is independent of leaf age and specific leaf area. There is evidence that in ryegrass, age has some effect on photosynthesis (Woledge & Leafe, 1976). Also, in fescue, it appears that  $P_m$  does depend upon specific leaf area (Woledge, 1971). Such effects are ignored in the present investigation.

The daily gross photosynthetic rate,  $P_d$ , is obtained by the integral

$$P_d = \int_0^h P_c dt, \quad (8)$$

where  $h$  is the daylength, s, and  $t$  is time, s. In order to evaluate this integral it is assumed that  $I_0$  is constant throughout the day, that is

$$I_0 = J/h, \quad (9)$$

where  $J (\text{J m}^{-2} \text{ d}^{-1} \text{ PAR})$  is the day's light receipt. Combining equations (7), (8) and (9) gives

$$P_d = \frac{P_m h}{k} \ln \left[ \frac{\alpha k J / h + (1-\tau) P_m}{\alpha k J \exp(-kL) / h + (1-\tau) P_m} \right], \quad (10)$$

for the daily gross photosynthetic integral, in units of  $\text{kg CO}_2 (\text{m}^2 \text{ of ground})^{-1} \text{ d}^{-1}$ . In terms of  $\text{kg carbon m}^{-2} \text{ d}^{-1}$ , the photosynthetic input to the model becomes

$$\theta P_d, \quad (11)$$

where  $\theta$  is a factor to convert  $\text{CO}_2$  to carbon.

#### Root growth and maintenance

In order to allow for root growth and maintenance, a fraction of the carbon fixed is allocated for shoot growth, the remainder being partitioned to the roots. Thus, of the total photosynthetic input given by equations (10) and (11), if the fraction available for shoot growth is  $\phi$ , then the carbon input to the shoot,  $P$ , is

$$P = \phi \theta P_d, \quad (12)$$

where  $\phi$  is dimensionless ( $0 < \phi < 1$ ).  $P$  has units  $\text{kg C} (\text{m}^2 \text{ of ground})^{-1} \text{ d}^{-1}$ .

#### Synthesis of structural material and respiration

Following Thornley & Hurd (1974), who give both experimental and theoretical justification for the assumption, the rate of synthesis of new structural material,  $G$ , is given by

$$G = \left( \frac{dW_G}{dt} \right)_{\text{gross}} = \mu \frac{W_s W_G}{W}, \quad (13)$$

with units  $\text{kg C m}^{-2} \text{ d}^{-1}$ .  $\mu (\text{d}^{-1})$  is a rate constant. This approach was used by Johnson *et al.* (1983) in a two-compartment grass growth model. A yield factor  $Y$  is defined as the units of structure that result from the use for synthesis of one unit of storage material, the rest being respired (typically,  $Y$  is approximately 0.75). Thus, the rate of utilization of storage for the production of new structure, given by (13), is

$$G/Y, \quad (14)$$

and the corresponding growth respiration  $R_g$  is

$$R_g = \left( \frac{1-Y}{Y} \right) G. \quad (15)$$

Maintenance costs are represented by a direct output from the storage compartment. Following McCree (1970), many workers have observed that maintenance respiration is proportional to the plant dry weight, although the constant of proportionality falls as the plant parts age (Penning de Vries, 1975). It is therefore assumed that the maintenance costs per unit dry weight vary between the different compartments so that the total maintenance respiration is given by

$$R_m = \sum_{i=1}^4 M_i W_i, \quad (16)$$

where the maintenance coefficients,  $M_i$  ( $i = 1, 2, 3, 4$ ), have units  $\text{d}^{-1}$ . It is assumed that the maintenance costs are always met, and hence if maintenance is interpreted in terms of degradation and re-synthesis of the structural components, this occurs at a rate

$$\frac{Y}{1-Y} M_i W_i. \quad (17)$$

#### Leaf area index

The new growth  $G$ , given by equations (13) and (14), is used either for producing new leaf or new sheath and stem. Thus, the rate of production of new leaf may be written as

$$\rho G, \quad (18)$$

where  $\rho$  ( $0 < \rho < 1$ ) is a dimensionless parameter. The corresponding rate of production of new sheath and stem is therefore

$$(1-\rho)G. \quad (19)$$

Robson (1973) observed that the ratio of leaf weight to sheath and stem weight is virtually constant over an entire growth period of experimentally simulated swards of perennial ryegrass and the data in his Fig. 3 suggest  $\rho = 0.7$ , which is consistent with observed field data (Parsons, personal communication). We therefore assume  $\rho$  to be constant, although for

crops where this is clearly not the case, modification of this assumption would be straightforward.

The rate of production of new leaf area, corresponding to the rate of production of new leaf weight given by equations (13), (14) and (18), is

$$\delta\rho G, \quad (20)$$

where  $\delta$  has units  $\text{m}^2$  of leaf  $(\text{kg C})^{-1}$  and may be regarded as the incremental specific leaf area. It has been observed that the leaf area/leaf weight ratio depends on the environment (Woledge & Jewiss, 1969; Woledge, 1971). However, it is unlikely that this is a direct dependence but, rather, the environment affects the state of the crop, in particular the relative amount of storage available for growth, which in turn affects the leaf area/leaf weight ratio. Thus, it is assumed that

$$\delta = \delta_m \left(1 - \zeta \frac{W_s}{W}\right), \quad (21)$$

where  $\zeta$  is a dimensionless parameter and  $\delta_m$  is the maximum value of  $\delta$ . This approach is generally consistent with experimental observations, although there are no data available to justify the specific form of equation (21) directly; hence we have chosen a simple equation to describe the relationship.

#### Senescence

Senescence is described by the flux of material out of the fourth compartment,  $W_4$ . Thus, the rate of senescence is

$$S = \gamma W_4, \quad (22)$$

with units  $\text{kg C m}^{-2} \text{ d}^{-1}$ .  $\gamma$  is a rate constant ( $\text{d}^{-1}$ ). This very simple representation of senescence assumes that only temperature has a direct immediate effect on the process (through  $\gamma$ ). Radiation has a delayed effect, as material has to work its way through the system. Other possibilities, such as a direct effect on the rate constant  $\gamma$  of daylength, irradiance or storage:structure ratio, have not been considered.

#### Flux of material between compartments

It is assumed that the fluxes of material from  $W_2$  to  $W_3$  and  $W_3$  to  $W_4$  also have rate constant  $\gamma$ . However, the weight of the average leaf passing from  $W_1$  to  $W_2$  will be considerably greater than the average leaf weight in  $W_1$  as this compartment comprises growing leaves. The flux of material into  $W_2$  is therefore given by

$$\lambda\gamma W_1, \quad (23)$$

where the dimensionless parameter  $\lambda$  allows for this difference. For example, with a linear distribution of leaf weights in  $W_1$  (that is, the number of leaves with weight in unit weight range is constant), then it follows that  $\lambda=2$ .

#### Effects of temperature

The rate parameter  $\gamma$ , the growth coefficient  $\mu$ , and the maintenance coefficients  $M_i$ ,  $i=1, 2, 3, 4$ , are assumed to increase with increasing temperature. Many authors have used  $Q_{10}$ -type equations to describe this temperature dependence, but we feel that the connection between reactions which obey this type of law and the complex processes involved in crop physiology do not justify the use of a  $Q_{10}$ -type equation. Instead, it is simply assumed that  $\gamma$ ,  $\mu$  and the maintenance coefficients obey a linear equation

$$X(T) = X(20) \frac{(T - T_0)}{(20 - T_0)}, \quad (24)$$

where  $T(\text{°C})$  is the mean daily temperature, and  $T_0$  is the temperature where crop growth effectively ceases.

Single leaf photosynthesis is likewise temperature dependent (Woledge & Dennis, 1981), although the effects diminish as the light level decreases. It is therefore assumed that  $P_m$ , in equation (7), also obeys equation (24).

We have chosen  $T_0=0^\circ\text{C}$  as the zero level for plant activity and have taken  $20^\circ\text{C}$  as the reference in equation (24) as this covers the temperature range for most practical situations. The temperature-dependent parameters will be time dependent through the time dependence of  $T$  (that is,  $T=T(t)$ ).

#### Mathematical summary of the model

The model has nine state variables:  $W_s$ ,  $W_1$ ,  $W_2$ ,  $W_3$ ,  $W_4$ ,  $L_1$ ,  $L_2$ ,  $L_3$ ,  $L_4$ , which are described by the differential equations

$$\frac{dW_s}{dt} = P - G/Y - R_m, \quad (25)$$

$$\frac{dW_1}{dt} = G - \lambda\gamma W_1, \quad (26a)$$

$$\frac{dW_2}{dt} = \lambda\gamma W_1 - \gamma W_2, \quad (26b)$$

$$\frac{dW_3}{dt} = \gamma W_2 - \gamma W_3, \quad (26c)$$

$$\frac{dW_4}{dt} = \gamma W_3 - \gamma W_4, \quad (26d)$$

$$\frac{dL_1}{dt} = \delta\rho G - \lambda\gamma L_1, \quad (27a)$$

$$\frac{dL_2}{dt} = \lambda\gamma L_1 - \gamma L_2, \quad (27b)$$

$$\frac{dL_3}{dt} = \gamma L_2 - \gamma L_3, \quad (27c)$$

$$\frac{dL_4}{dt} = \gamma L_3 - \gamma L_4. \quad (27d)$$

$P$  is given by equations (10) and (12),  $G$  by equation (13),  $R_m$  by equation (16) and  $\delta$  by equation (21). There are nine equations altogether, but they are simple and similar in structure. The model has eighteen parameters:  $k$ ,  $\tau$ ,  $\alpha$ ,  $P_m$ ,  $\theta$ ,  $\phi$ ,  $\mu(20)$ ,  $Y$ ,  $M_i$  ( $i = 1, 2, 3, 4$ ),  $\rho$ ,  $\delta_m$ ,  $\zeta$ ,  $\gamma(20)$ ,  $\lambda$  and  $T_0$ . The environmental inputs are  $J$ ,  $T$  and  $h$ . All state variables, parameters and environmental inputs are listed in the Appendix along with units and values used (in the cases where their values are fixed).

Adding equation (25) and (26), the total mass balance is given by

$$\frac{dW}{dt} = P - R_g - R_m - S, \quad (28)$$

where  $R_g$ ,  $R_m$  and  $S$  are given by equations (15), (16) and (22) respectively.

Initial conditions for each of the nine differential equations must be provided in order to solve the equations subject to given environmental conditions.

## Results and discussion

In the model there is no account of diurnal fluctuations; the daily total of gross photosynthesis is calculated over the light period, which is then assumed to be distributed uniformly over 24 h. This approach simplifies the problem considerably, without affecting materially the crop responses of interest. Equations (25), (26), and (27) are therefore differential equations (not difference equations), and numerical solutions to the model were obtained using CSMP (Continuous System Modelling Program). Unless otherwise stated, the initial conditions adopted were

$$W_S = 0.015 \text{ kg carbon m}^{-2}, \quad (29a)$$

$$W_1 = W_2 = W_3 = W_4 = 0.02 \text{ kg carbon m}^{-2}, \quad (29b)$$

$$L_1 = L_2 = L_3 = L_4 = 0.2. \quad (29c)$$

The parameter values used are given in the Appendix.

The effect of changing the incident light flux density,  $J$ , is predictable; an increase in  $J$  causes an increase in photosynthesis and hence greater yield. Less predictable is the effect of changing the mean daily temperature,  $T$ , as this affects the flux of carbon both into and out of the system. Consequently, high temperature does not necessarily imply high yield. In Fig. 2 the solutions are given for  $T = (5, 10, 15)^\circ\text{C}$ , with  $J = 8 \times 10^6 \text{ J m}^{-2} \text{ d}^{-1}$  and  $h = 54 \times 10^3 \text{ s}$  ( $\equiv 15$  h). This value for  $J$  is typical of good summer weather at Hurley. During the early stages of growth there is better growth at higher temperature, although the difference between 10 and  $15^\circ\text{C}$  is small. However, the ceiling yield increases with decreasing temperature. In Fig. 3 the equivalent curves with  $J = 4 \times 10^6 \text{ J m}^{-2} \text{ d}^{-1}$  are drawn and it is apparent that at lower light levels, higher temperatures are actually deleterious to growth and

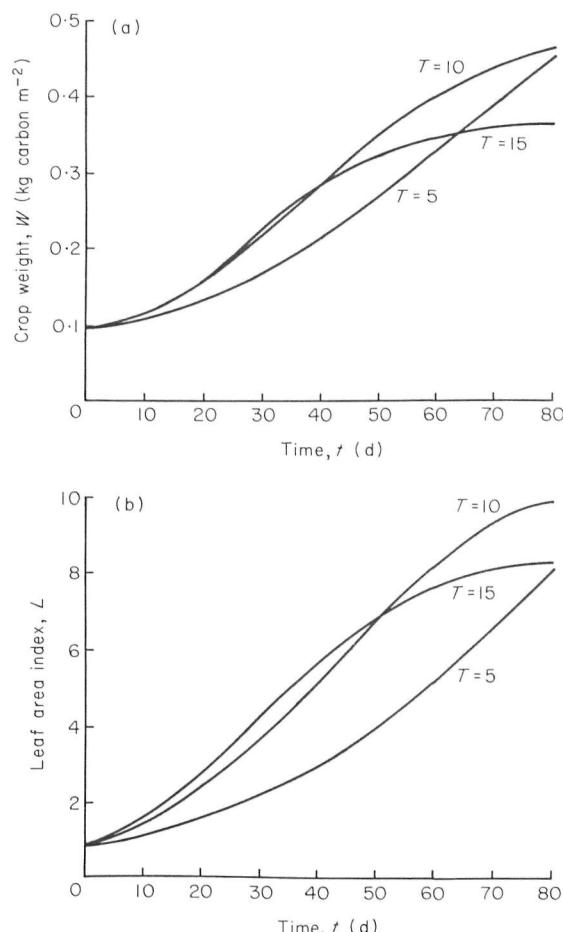


Figure 2. Above-ground crop weight and leaf area index with  $J = 8 \times 10^6 \text{ J m}^{-2} \text{ d}^{-1}$ ,  $h = 54 \times 10^3 \text{ s}$  (15 h), and  $T = (5, 10, 15)^\circ\text{C}$ .

yield, as is well-known with many glasshouse crops. In a set of controlled environment experiments on simulated swards of perennial ryegrass, Robson (1973) observed that the only noticeable effect of reducing temperature was to increase the ceiling yield (see his Fig. 8b). It should be pointed out that his swards were grown from seed and so the initial conditions given by equations (29) and the assumption of a constant proportion of photosynthesis being partitioned to the roots will not be strictly valid. However, the resultant trend should be similar. This temperature effect may not necessarily be observed with spaced plants where virtually all the photosynthesizing leaves will benefit from an increase in temperature.

The crop growth rates,  $dW/dt$ , corresponding to the illustrations in Fig. 2 are shown in Fig. 4, and the gross photosynthetic rates available for shoot growth [given by equations (10) and (12)] are illustrated in Fig. 5. The effects of temperature are more evident here than in Fig. 2. Note that for  $T = 10, 15^\circ\text{C}$ , when the canopy is virtually fully light intercepting the difference in the final values of  $P$  (Fig. 5) is due to temperature only.

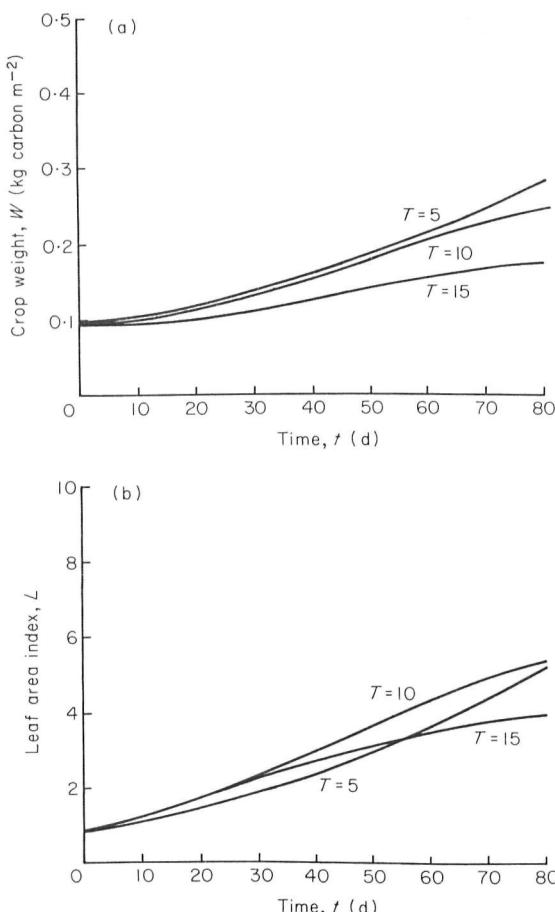


Figure 3. Above-ground crop weight and leaf area index with  $J=4 \times 10^6 \text{ J m}^{-2} \text{ d}^{-1}$ ,  $h=54 \times 10^3 \text{ s}$  (15 h), and  $T=(5, 10, 15)^\circ\text{C}$ .

Of especial interest is the fraction of storage,  $W_S/W$ . This ratio is shown in Fig. 6, again corresponding to the growth curves in Fig. 2. At 10 and  $15^\circ\text{C}$ , early substrate use reduces the storage pool, but the subsequent balance between photosynthesis and growth then gives rise to an increase. Such behaviour is discussed by Milthorpe & Davidson (1966). At  $5^\circ\text{C}$  the early reduction in storage does not occur due to the reduced rate of storage utilization. As shading becomes significant the photosynthesis per unit plant weight decreases, yet this is not the case with the demand for growth and maintenance. Consequently  $W_S/W$  falls. This trend in storage levels has been observed in tomatoes (Cooper & Thornley, 1979; Ho & Shaw, 1979), in soybean (Dunphy & Hanway, 1976) and in grasses (Waite & Boyd, 1953). For the crop grown in low light (Fig. 3), the pattern of storage was the same but the levels were lower.

The initial LAI value is important as it controls the photosynthetic capacity of the crop after defoliation. To show the effects of severe defoliation, Fig. 7 compares the growth curve illustrated in Fig. 2 for  $T = 15^\circ\text{C}$  ( $J = 8 \times 10^6 \text{ J m}^{-2} \text{ d}^{-1}$ ,

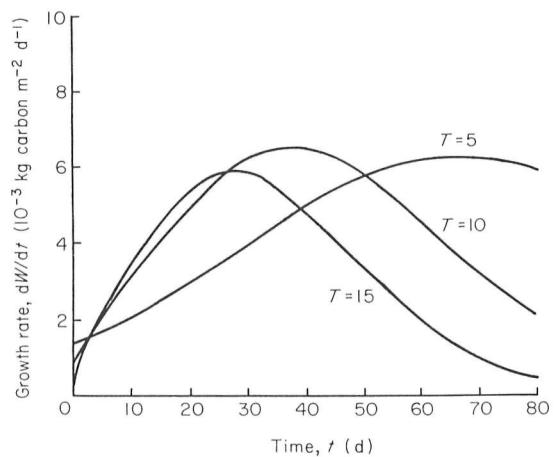


Figure 4. Above-ground crop growth rates corresponding to the growth curves illustrated in Fig. 2.

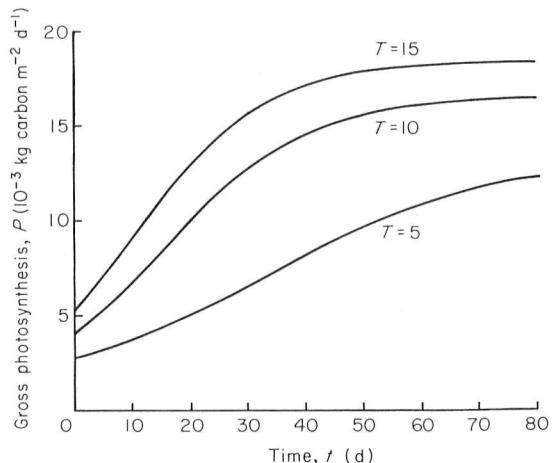


Figure 5. Gross photosynthetic rate available for shoot growth corresponding to the growth curves illustrated in Fig. 2.

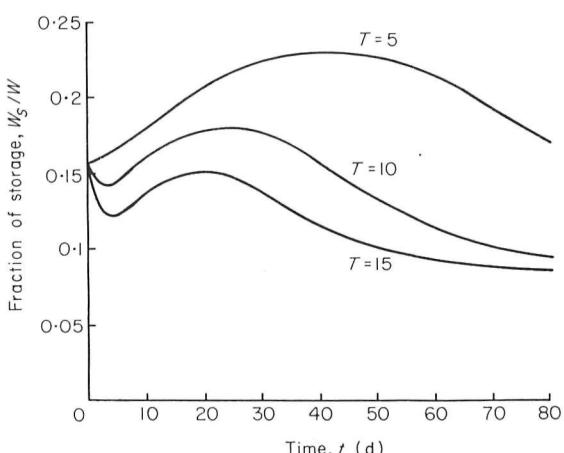
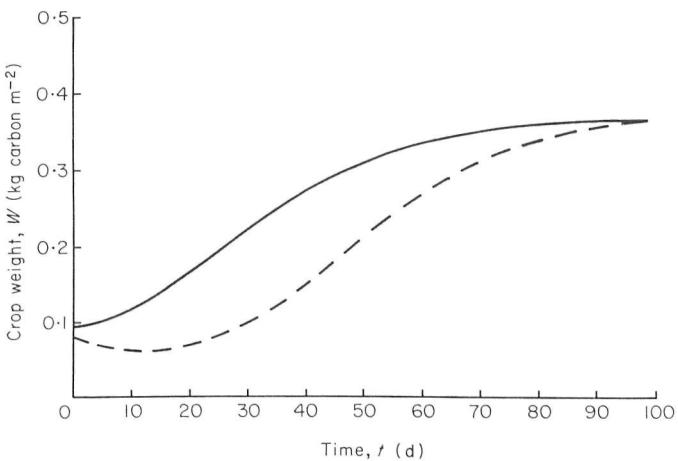


Figure 6. Ratio of storage to total weight,  $W_S/W$ , corresponding to the growth curves illustrated in Fig. 2.



**Figure 7.** Simulation of severe defoliation, using different initial values of the leaf area index for  $T = 15^\circ\text{C}$ ,  $J = 8 \times 10^6 \text{ J m}^{-2} \text{ d}^{-1}$ ,  $h = 54 \times 10^3 \text{ s}$  (15 h). Continuous line  $L(t=0) = 0.8$ , dashed line  $L(t=0) = 0.01$ . See text for details.

$h = 54 \times 10^3 \text{ s} \equiv 15 \text{ h}$ ) with that obtained with a very small LAI at  $t=0$ :

$$L_1 = 0.01, \quad L_2 = L_3 = L_4 = 0, \quad (30)$$

with the weight components scaled accordingly. This extreme example illustrates the point that the crop utilizes its resources to produce new leaves, with an initial loss in weight. After recovery, the two curves are virtually identical, apart from the time lag. This time lag is particularly noticeable after severe defoliation of the reproductive crop during early summer at the start of the first vegetative growth period (Leafe, Stiles & Dickinson, 1974): since the stems elongate during the reproductive phase, most of the leaf area will be removed at this first harvest, more so than after harvesting a vegetative crop.

The simulations have so far been for a constant environment. To examine the effect of seasonal variation in the environmental parameters, the following equations, obtained from fitting several years' data at Hurley, were used for  $J$  and  $T$ , and an approximate equation for  $h$ :

$$J \times 10^{-6} = 0.7 + 8.2 \sin^2 \left\{ \frac{\pi(t+10)}{365} \right\}, \quad (31a)$$

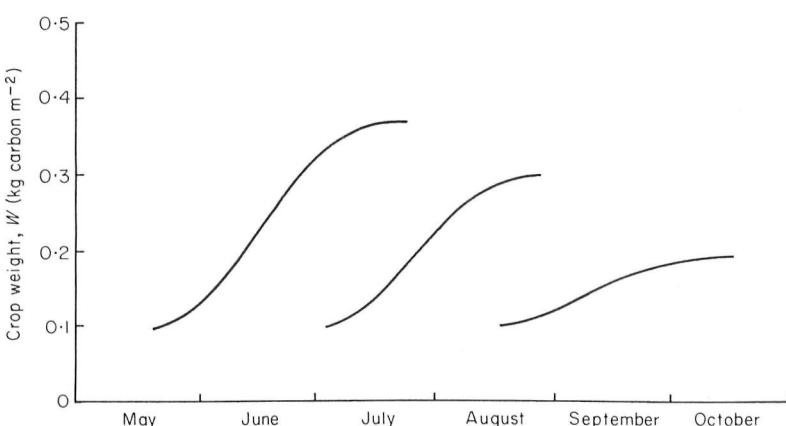
$$T = 3.2 + 12.7 \sin^2 \left\{ \frac{\pi(t-24)}{365} \right\}, \quad (31b)$$

$$h = 28,800 \left[ 1 + \sin^2 \left\{ \frac{\pi(t+10)}{365} \right\} \right], \quad (31c)$$

where  $t$  is measured from 1 January. Note that  $28,800 \text{ s} \equiv 8 \text{ h}$ . The seasonal pattern of vegetative growth is illustrated in Fig. 8 [with the initial conditions again given by equations (29)]. These curves are typical of those obtained for the vegetative grass crop (Leafe *et al.*, 1974)

### Conclusions

While the model is able to simulate the general features of the vegetative grass crop, it could be applied to some other vegetative crops with appropriate parameter values. One of its main innovative features is that LAI is an independent



**Figure 8.** Seasonal pattern of vegetative growth.

state variable, and is not, as in many crop models, inflexibly related to crop dry weight by an empirical equation. This produces extremely robust and adaptable behaviour, as demonstrated by the grass crop, and shown in the illustrations. Another important feature is the way in which the storage pool is used to control incremental specific leaf area, in addition to its more familiar roles of providing a buffer against environmental fluctuations and controlling the rate of production of new growth. Although the model is restricted to the vegetative crop, it seems likely that this approach, suitably modified, might be applied equally successfully to a reproductive crop.

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### Appendix: Definition of symbols

#### Independent variable

<i>t</i>	Time	day (d)
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#### State variables

$L_i$ , $i=1-4$	Components of leaf area index [equation (3)]	$m^2$ (leaf) $m^{-2}$ (ground)
$W_i$ , $i=1-4$	Components of structural dry weight [equation (1)]	$kg$ carbon $m^{-2}$
$W_s$	Storage dry weight [equation (2)]	$kg$ carbon $m^{-2}$

#### Other variables

$G$	Rate of production of new structure [equation (13)]	$kg$ carbon $m^{-2} d^{-1}$
$I$	Instantaneous downward light flux density in the canopy at leaf area index $L$ [equation (4)]	$W m^{-2}$
$I_1$	Instantaneous light flux density on the leaves at leaf area index $L$ [equation (5)]	$W m^{-2}$ (leaf)
$L$	Leaf area index of crop [equation (3)]	$m^2$ (leaf) $m^{-2}$ (ground)
$M_i$ , $i=1-4$	Maintenance respiration co- efficients [equation (16)]	$d^{-1}$
$P$	Total daily photosynthetic input available for shoot growth [equation (12)]	$kg$ carbon $m^{-2} d^{-1}$
$P_c$	Canopy gross photosynthetic rate [equation (7)]	$kg CO_2$ $m^{-2} s^{-1}$

$P_d$	Daily gross photosynthetic rate [equation (8)]	$kg CO_2$ $m^{-2} d^{-1}$
$P_g$	Single leaf gross photosynthetic rate [equation (6)]	$kg CO_2$ $m^{-2}$ (leaf) $s^{-1}$
$P_m$	Light-saturated leaf gross photosynthetic rate [equation (6)]	$kg CO_2$ $m^{-2}$ (leaf) $s^{-1}$
$R_g$	Growth respiration [equation (15)]	$kg$ carbon $m^{-2} d^{-1}$
$R_m$	Maintenance respiration [equation (16)]	$kg$ carbon $m^{-2} d^{-1}$
$W$	Total crop dry weight [equation (2)]	$kg$ carbon $m^{-2}$
$W_G$	Total structural dry weight [equation (1)]	$kg$ carbon $m^{-2}$
$\gamma$	Rate of leaf appearance per tiller [equation (22)]	$d^{-1}$
$\delta$	Incremental specific leaf area [equation (20)]	$m^2$ (leaf) (kg carbon) $^{-1}$
$\mu$	Growth coefficient [equation (13)]	$d^{-1}$

#### Plant parameters

$k$	Extinction coefficient of canopy [equation (4)]	0.5
$M_1(20)$	Maintenance respiration	$0.02 d^{-1}$
$M_2(20)$	coefficients at $20^\circ C$ [equation	$0.02 d^{-1}$
$M_3(20)$	(24)]	$0.15 d^{-1}$
$M_4(20)$		$0.01 d^{-1}$
$P_m(20)$	Light-saturated gross photosynthetic rate at $20^\circ C$ [equation (24)]	$1.5 \times 10^{-6}$ $kg CO_2$ $m^{-2} s^{-1}$
$T_0$	Temperature at which crop growth ceases [equation (24)]	$0^\circ C$
$Y$	Yield factor [equation (14)]	0.75
$\alpha$	Leaf photosynthetic efficiency [equation (6)]	$12 \times 10^{-9}$ $CO_2 J^{-1}$
$\gamma(20)$	Rate of leaf appearance at $20^\circ C$ [equation (24)]	$0.15 d^{-1}$
$\delta_m$	Incremental specific leaf area parameter [equation (21)]	$40 m^2$ (leaf) (kg carbon) $^{-1}$
$\zeta$	Incremental specific leaf area parameter [equation (21)]	1
$\theta$	Conversion factor from $CO_2$ to carbon; taken to be the ratio of the relative molecular masses of carbon to $CO_2$ [equation (11)]	$12/44$ kg carbon (kg $CO_2$ ) $^{-1}$
$\lambda$	Weighting factor for flux of material from first to second compartment [equation (23)]	2
$\mu(20)$	Growth coefficient at $20^\circ C$ [equation (24)]	$0.5 d^{-1}$
$\rho$	Fraction of new growth partitioned to leaf growth [equation (18)]	0.7

$\tau$	Leaf transmission coefficient [equation (5)]	0.1
$\phi$	Proportion of carbon fixed by photosynthesis available for shoot growth [equation (12)]	0.9
<i>Environmental quantities</i>		
$h$	Daylength [equation (8)]	$s(d)^{-1}$
$I_0$	Instantaneous light flux density above the canopy [equation (4)]	$W m^{-2}$
$J$	Daily energy (PAR) receipt [equation (9)]	$J m^{-2} d^{-1}$
$T$	Mean daily temperature [equation (24)]	$^{\circ}C$

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