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Acta Agriculturae Scandinavica

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t914430183>

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To cite this Article Hansen, G. K. and Svendsen, H. (1986) 'A Model of Assimilate Partitioning and Utilization in Shoots and Roots in the Vegetative Stage of *Lolium multiflorum*', Acta Agriculturae Scandinavica, 36: 3, 286 – 300

To link to this Article: DOI: 10.1080/00015128609436531

URL: <http://dx.doi.org/10.1080/00015128609436531>

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A Model of Assimilate Partitioning and Utilization in Shoots and Roots in the Vegetative Stage of *Lolium multiflorum*

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Hansen, G. K. & Svendsen, H. (Institute of Crop Husbandry & Plant Breeding, Royal Veterinary & Agricultural University, Agrovej 10, DK-2630 Taastrup, Denmark). A model of assimilate partitioning and utilization in shoots and roots in the vegetative stage of *Lolium multiflorum*. Received Nov. 15, 1985. Acta Agric Scand 36: 286–300, 1986.

With the purpose of improving crop growth simulation, a mechanistic model and its parameters for assimilate partitioning and utilization were developed for vegetative *Lolium multiflorum* Lam. (cv. Lomi). The model is based on first-order kinetics and on previously determined efficiencies of assimilate utilization. The driving variable is gross photosynthesis. The five state variables are the translocation pool of recently assimilated carbon, and for shoots and roots, the storage pools and the pools of structural material, respectively. The model consists of first-order rate equations with six parameters. These parameters were estimated by analysis of the time course of CO₂-exchange rates, separately for shoots and roots, respectively, during prolonged dark periods of two days and prolonged photoperiods of two days. The analysis was based on maintenance coefficients and on utilization efficiencies of shoots and roots and on simulation. Due to the differences in carbon utilization between shoots and roots it was concluded that environmental factors influencing the respiration will cause changes in the shoot:root relation. Thus predicted data showed that the functional relation: "shoot weight × shoot activity = root weight × root activity" may be explained by the differences between shoot and root respiration. *Key words: Photosynthesis, respiration, translocation, storage and structural plant material.*

INTRODUCTION

Growth of shoots and roots depends on photosynthetic supply, partitioning and utilization of assimilate. For model purpose plants are often considered as consisting of two carbon components, structural and storage material (Warren Wilson, 1972). Structural materials can be further divided in degradable and non-degradable material (Thornley, 1977). As utilization of assimilates for growth and maintenance differs for shoots and roots (e.g. Hansen & Jensen, 1977; Hansen, 1978; Lambers, 1979; Farrar, 1980) partitioning should be related to the flow of carbon rather than on determination of the relation between shoot and root dry matter. The model for vegetative plant growth of Thornley (1977) was based on the concept that respiration is directly proportional to rate of conversion of storage material into structural material and this rate is proportional to the amount of storage material. A part of the structural material is degradable and recycled through the pool of storage material. Barnes & Hole (1978) showed that Thornley's (1977) model did not conflict with the general assumptions that respiration can be divided functionally into two components, growth and maintenance. There were, however, difficulties in estimating parameters of the model, as the initial values of the different pools usually are not known.

The present work was an attempt to estimate for shoots and roots the parameters of the model of Thornley (1977) and the parameters of assimilate partitioning between shoots and roots. The analyses were based on separate and simultaneous measurements of CO₂-effluxes from shoots and roots in darkness of *Lolium multiflorum* (Lam) cv. Lomi. All

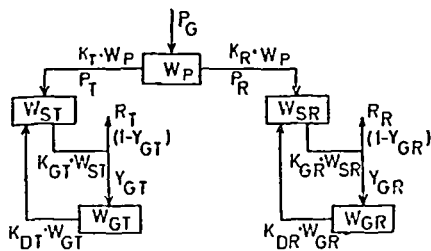


Fig. 1. The model for partitioning and utilization of carbon. Boxes are state variables, arrows flows. *T* and *R* indicate shoots and roots, respectively.

fluxes considered are carbon compounds lumped together. Furthermore the straightforward simulation model has the purpose of explaining the consequences of different carbon utilization in shoots and roots as found by Hansen & Jensen (1977) and Hansen (1978). An important aim was to construct a submodel applicable for crop simulation models.

The model

The model has five state variables (Fig. 1): The pool of recently assimilated carbon, W_P , for shoots and roots the storage pools, W_{ST} and W_{SR} , and the structural material W_{GT} and W_{GR} , respectively. The latter were divided into degradable and non-degradable material in Thornley's (1977) model, but here they are not.

Furthermore the model consists of six first-order rate constants, the partitioning constants K_T and K_R , the constants for conversion of W_S into W_G , K_{GT} and K_{GR} , and the rate constants of degradation K_{DT} and K_{DR} . The subscripts *T* and *R* denote shoots and roots, respectively.

Supply of assimilates is P_G , net photosynthesis plus mitochondrial respiration of shoots, and is the driving variable of the model.

Shoot dry matter

$$W_T = W_{ST} + W_{GT} + W_P \quad (1)$$

and root dry matter

$$W_R = W_{SR} + W_{GR} \quad (2)$$

The rates of changes of the pools are described by equations (3–7). The rate of change of the pool of recently assimilated carbon is

$$\frac{dW_P}{dt} = P_G - P_T - P_R \quad (3)$$

where P_R and P_T are rates of carbon translocation from the transport pool to the storage pools of roots and shoots, respectively.

The rates of change of storage and structural carbon of shoots are

$$\frac{dW_{ST}}{dt} = P_T - K_{GT} W_{ST} + K_{DT} W_{GT} \quad (4)$$

and

$$\frac{dW_{GT}}{dt} = Y_{GT} K_{GT} W_{ST} - K_{DT} W_{GT} \quad (5)$$

The corresponding rates for roots are

$$\frac{dW_{SR}}{dt} = P_R - K_{GR} W_{SR} + K_{DR} W_{GR} \quad (6)$$

and

$$\frac{dW_{GR}}{dt} = Y_{GR} K_{GR} W_{SR} - K_{DR} W_{GR} \quad (7)$$

The assimilate fluxes, P_T and P_R , to the two storage pools are

$$P_T = K_T W_P \quad (8)$$

and

$$P_R = K_R W_P \quad (9)$$

The model does not distinguish explicitly between growth and maintenance respirations as they use the same substrate. The total respiration for shoots, R_T , and for roots R_R , consists of the sum of the two terms and is proportional to the amount of storage material expressed by:

$$R_T = (1 - Y_{GT}) K_{GT} W_{ST} \quad (10)$$

and

$$R_R = (1 - Y_{GR}) K_{GR} W_{SR} \quad (11)$$

Y_{GT} and Y_{GR} are efficiencies of conversion storage material into structural material, and assumed to be constant.

MATERIALS AND METHODS

The experiments

The method of CO_2 -exchange measurements was described previously (Hansen & Jensen, 1977). Ten plants of *Lolium multiflorum* cv. Lomi in each pot were grown under controlled conditions at 20°C in a modified Hoagland solution at 16 h photoperiod and 8 h darkness. Five weeks old they were placed into assimilation chambers, allowing separate measurements of CO_2 -exchange rate for shoots and roots. To avoid absorption of CO_2 in the nutrient solution a cation resin "Amberlite IRC 50" was placed in the nutrient solution ensuring pH between 4.5 and 4.8.

In one of the experiments (exp. 1) the plants after accomplishing normal diurnal cycle, were placed in darkness for 48 h, after which they were placed in light of 145 W m^{-2} (400–700 nm) for 48 h. In the other experiment (exp. 2) the plants initially were placed in continuous light for 48 h, followed by 48 h of continuous darkness. The lamps were Philips HPI 400 Watt.

During the two periods CO_2 -exchange rates were measured every 20 min. Temperature was kept constant at 20°C. The initial dry matter weights were calculated, from the measured CO_2 -uptake and harvested dry matter at the end of the experiment.

Parameter estimation 1: Y_G , M and K_D

In the following, the subscripts T and R are omitted. Based on diurnal values of carbon balances, the growth and maintenance respiration of shoots and roots, respectively, were estimated for *Lolium multiflorum* (Hansen, 1978) by multiple regression and application of eq. (12).

$$R = (1 - Y_G) \Delta W_S + M W_G \quad (12)$$

The first term is growth respiration and the second maintenance respiration. W_S is the diurnal contribution of W_S to growth of structural materials and M is the maintenance coefficient.

The relation between W_S and R is given by eq. (10) and by combination and rearrangement of eqs. (5) and (10).

$$R = \frac{1 - Y_G}{Y_G} \left[\frac{dW_G}{dt} + K_D W_G \right] \quad (13)$$

When $dW_G/dt = 0$ ($t = t_m$), then from eqs. (10) (or 11) and (13)

$$K_D = \frac{Y_G K_G W_S}{W_G} \quad (14)$$

Maintenance respiration defined as the respiration needed to maintain *status quo* of structural material is equal to the respiration at $t = t_m$ is given by:

$$R_M = M W_G \quad (15)$$

By combination of (13) and (15)

$$K_D = \frac{Y_G M}{1 - Y_G} \quad (16)$$

Eq. (16) gives the relation between K_D and M , and shows how the maintenance coefficient M is related to the degradation of W_G .

Parameter estimation 2: K_G

The parameters K_G were estimated from the measurements of the respiration rates during prolonged dark periods (Fig. 2). After a while in darkness the fluxes from the transport pool vanish. Then dW_S/dt becomes negative, i.e. the storage materials decline and therefore respiration will decline, too. Respiration is equal to maintenance respiration when $t = t_m$. At this time no changes in structural materials occur, i.e. $dW_G/dt = 0$. At $t < t_m$ structural materials are still increasing, i.e. $dW_G/dt > 0$. When $t > t_m$, the structural materials decrease, i.e. $dW_G/dt < 0$. When the fluxes from the transport pool vanish, then according to Thornley (1977):

$$W_S = B \exp(\lambda_1 t) + C \exp(\lambda_2 t) \quad (17)$$

when B and C are constants depending on the initial values of W_S and λ_1 and λ_2 are eigenvalues.

The four constants of eq. (17) are difficult to find from the declining respiration rates due to scatter of the experimental results. Therefore eq. (17) was only used for curve fitting of the results.

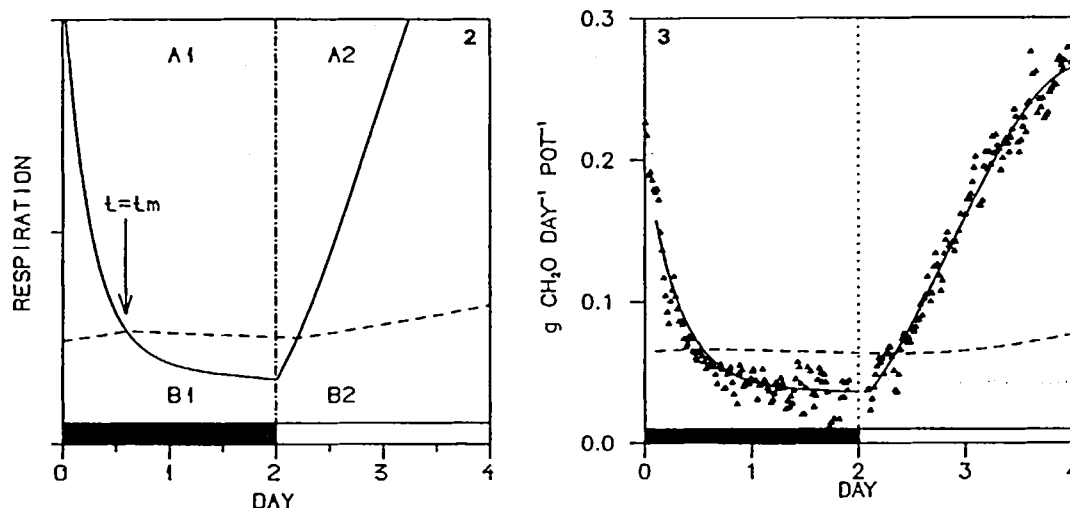


Fig. 2. The principal time course of respiration rates during a dark period followed by a photoperiod. t_m is the time when respiration is equal to maintenance respiration (---). During the dark period (A 1, B 1) $dW_s/dt < 0$. When respiration > maintenance respiration (A 1, A 2) then $dW_s/dt > 0$, and when respiration < maintenance respiration (B 1, B 2), then $dW_s/dt < 0$.

Fig. 3. Measured root respiration during two days of darkness (black bar) and following two-day photoperiod (white bar). (—), results simulated by the model; (---), estimated maintenance respiration.

The rate of change of total dry matter, W , beyond minerals was obtained from the continuous measurements of CO₂-exchange rates by

$$P_G - R = \frac{dW}{dt} = \frac{dW_s}{dt} + \frac{dW_G}{dt} \quad (18)$$

From the continuous measurements of CO₂-exchange rates, W could at any time during a period be found from the final harvested dry matter weight and its carbon content. By combination of eqs. (1), (10), and (13) for shoots or eqs. (2), (11), and (13) for roots then

$$R = \frac{(1 - Y_G)}{Y_G} \frac{dW_G}{dt} + M \left[W - \frac{R}{K_G(1 - Y_G)} \right] \quad (19)$$

With $P_G = 0$, then at any time W could be found by integration of (18)

$$W = W_0 - \int_0^t R dt \quad (20)$$

where W_0 is the initial amount of dry matter.

Differentiation of eq. (10) with respect to time and combining with eq. (18) gives

$$K_G(1 - Y_G) = \frac{-dR}{R + \frac{dW_G}{dt}} \quad (21)$$

By combining of eqs. (19), (20), and (21) then

$$\frac{dW_G}{dt} = \frac{\left\{ R - M \left[W_0 - \int_0^t R dt \right] \right\} \frac{dR}{dt} - MR^2}{\frac{(1-Y_G)}{Y_G} \frac{dR}{dt} + MR} \quad (22)$$

By application of eq. (22) the time t_m , where $dW_G/dt=0$, was estimated by the second method. From eq. (21) it follows that at $t=t_m$, $dW_G/dt=0$ and

$$K_G = \frac{-1}{(1-Y_G)} \left[\frac{\frac{dR}{dt}}{R} \right]_{(t=t_m)} \quad (23)$$

Parameter estimation 3: K_T and K_R

In the fotoperiod root respiration and net CO_2 -uptake, P_N , of shoots were measured. Shoot respiration had to be simulated, assuming no changes from darkness to light condition. Measured root respiration and net CO_2 -uptake was the driving variables for the simulation. After a prolonged period of darkness the time course of root respiration was empirically fitted by

$$R_R = A_1 + A_2 t + A_3 t^2 + A_4 t^3 \quad (24)$$

It was feasible to estimate the partitioning constants K_T and K_R by simulation. The time intervals used in the simulation were those of the measurements of P_N . The basis for this simulation is given in the following.

By solving eq. (6) with respect to P_R then

$$P_R = \frac{dW_{SR}}{dt} + K_{GR} W_{SR} - K_{DR} W_{GR} \quad (25)$$

From (11) follows that

$$W_{SR} = \frac{R_R}{(1-Y_{GR}) K_{GR}} \quad (26)$$

which differentiated gives

$$\frac{dW_{SR}}{dt} = \frac{1}{(1-Y_{GR}) K_{GR}} \frac{dR_R}{dt} \quad (27)$$

where dR_R/dt can be found by differentiation of eq. (24).

By substitution of eqs. (26) and (27) into eqs. (7) and (25)

$$P_R = \frac{1}{K_{GR}(1-Y_{GR})} \frac{dR_R}{dt} + \frac{1}{(1-Y_{GR})} R_R - K_{DR} W_{GR} \quad (28)$$

and

$$\frac{dW_{GR}}{dt} = \frac{Y_{GR}}{(1-Y_{GR})} R_R - K_{DR} W_{GR} \quad (29)$$

Assuming that the relation between shoot and root partitioning was constant and independent of time, then

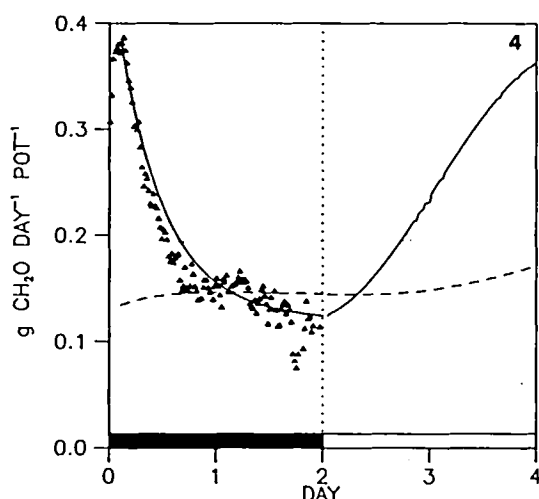


Fig. 4. Measured shoot respiration during two days of darkness (black bar). (—), results simulated by the model; (---), estimated maintenance respiration.

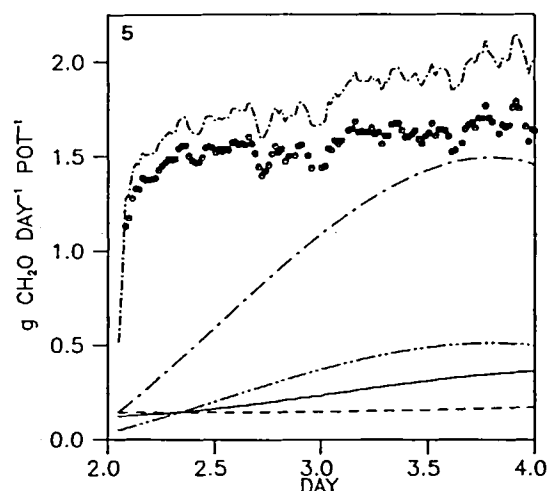


Fig. 5. The prolonged photoperiod after the two days of darkness: measured net CO_2 -uptake in CH_2O equivalents (●), and estimated P_G (·-·), P_T (-·-), P_R (- - -), R_T (—), and R_{MT} (---).

$$\frac{P_T}{P_R} = K_P \quad (30)$$

P_T could be found.

The processes and conditions of the shoots follow eqs. (4) and (5) with the belonging initial values. The time intervals were 0.014 day, being that of the frequency of measurements.

The "gross photosynthesis" was found from

$$P_G = P_N + R_T \quad (31)$$

The change of the pool of recently assimilated carbohydrates was simulated by application of eq. (3) and R_T by application of eq. (10).

The needed initial values for the simulation were: W_{PO} , W_{STO} , W_{SRO} , W_{GRO} . The parameters needed were K_{GT} , K_{GR} , K_{DT} , and K_{DR} , the eqs. (3), (4), (5), (27), (28), (29), and (31) and an initial value of K_P in eq. (30). By trial and error, a value K_P satisfying $K_P = (P_G - P_R)/P_R$ and $K_P = P_T/(P_G - P_T)$ was found. This occurred at the time where P_T and P_R had reached a maximum level. Then the parameters K_T and K_R were found by linear regression between simulated values of P_T and P_R , respectively, and W_P .

RESULTS

The courses of shoot and root respiration during the dark period (Figs. 3 and 4) showed the double exponential decays (eq. 5).

After near 11 hours of darkness, root respiration was equal to the estimated maintenance respiration, and it continued to decrease below this level. From the commencement of the photoperiod it increased and became equal to maintenance respiration after near 10

hours of light. After 48 hours of continuous light it levelled out. The simulated courses of root respiration rates followed the measured ones.

Shoot respiration was equal to the estimated maintenance respiration after 25 hours of darkness, and continued to decrease. Only simulated results were obtainable during the photoperiod, and showed a course analogous to that for roots. During darkness, simulated results appeared to be a little too high, as compared with the measured ones. Small oscillations of the simulated results were caused by the scatter of the measured net CO_2 -uptake, which was the driving variable of the simulation. From rates below maintenance respiration the simulation showed that this was again obtained after 7 hours in the light. After 48 hours in the light respiration was three times as high as maintenance respiration.

On the basis of the declining courses of respiration rates and by known values of Y_G and M previously determined (Hansen, 1978) the values of K_G were estimated, and K_D values were found from eq. (11) (Table 1).

For shoots and roots the ratio $K_G:K_D$ were 14.5 and 40.5, respectively, which indicates the stability of the structural materials compared with the storage material. The time ($t=t_m$) at which $dW_G/dt=0$ was shorter for roots than for shoots (Table 1).

The estimations of K_G were very sensitive to the estimated initial dry weight. Change of 1% in initial dry weight resulted in changes of 5% in K_G .

Root respiration rates of exp. 1 during the 48 h photoperiod after the period of darkness was fitted by eq. 24 from which dR_R/dt and P_R was found. In this period shoot respiration was simulated (Fig. 4) on the basis of measured net CO_2 -uptake of shoots (Fig. 5) and root respiration.

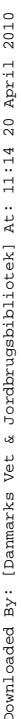
The value of W_{ST} , at the beginning of the photoperiod, was found from eq. (6) using the measured shoot respiration rate just before the onset of light. Root respiration increased but was delayed relatively to net CO_2 -uptake by the shoots. The simulated values of P_T were based on the assumption that the relation between P_T and P_R remained constant during the time course, being that obtained at steady state after near 48 h in the continuous photoperiod. The ratio between the first order rate partitioning constants, $K_T:K_R$, was 2.85 (Table 1).

Simulation 1: Comparisons with experimental results

Simulated results of respiration, growth of shoots and roots were compared with results from Hansen (1978), where CO_2 -fluxes were continuously and separately measured during 52 days with intervals of about 20 min. After 20 days the shoots were cut leaving a stubble height of 2 cm. In this simulation, the driving variable was measured net CO_2 -uptake. Temperature was kept around 20°C. Two or three days of high (145 W m^{-2}) and low (25 W m^{-2}) photosynthetically active light alternated.

Table 1. The values of parameters for shoots and roots from the two experiments, W_O , the initial dry matter, t_m , the time at which respiration (in darkness) was equal to maintenance respiration, the parameters K_G , K_D , K_T , and K_R . Y_G and M are the values from Hansen (1978)

Experi- ment	Organ	W_O (g pot ⁻¹)	t_m (day)	K_G (day ⁻¹)	K_D (day ⁻¹)	K_T (day ⁻¹)	K_R (day ⁻¹)	Y_G	M (day ⁻¹)
1	Shoots	5.35	1.025	2.2	0.151	0.70	—	0.83	0.31
	Roots	1.11	0.445	3.2	0.079	—	0.24	0.54	0.65
2	Shoots	6.70	0.705	2.2	0.151	—	—	0.83	0.31
	Roots	1.60	0.405	3.2	0.079	—	—	0.54	0.65

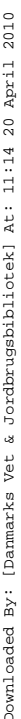


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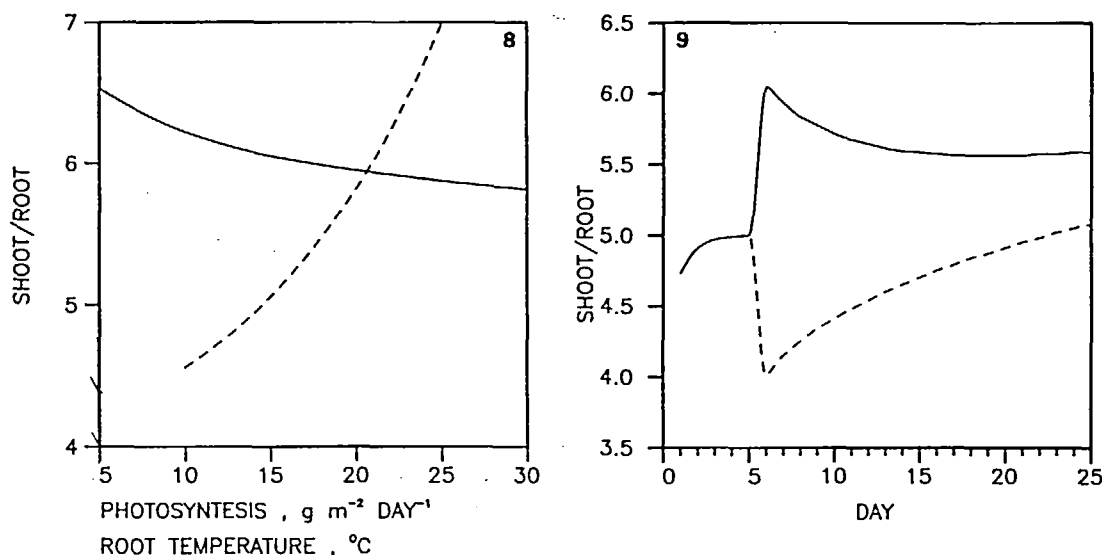


Fig. 8. Simulated shoot:root dry matter ratio after 25 days at varying gross photosynthesis with constant temperature (20°C) (—), and with varying root temperature with constant photosynthesis (20 g CH₂O m⁻² day⁻¹) (---). Initial conditions (g m⁻²): $W_{ST}=20$, $W_{GT}=160$, $W_{SR}=10$, $W_{GR}=26$. The photoperiod was 16 h.

Fig. 9. Simulated influence of shoot cutting (---) and root pruning (—) on the time course of shoot:root ratio. Up to the day of interference (day 5), the conditions were as those given in Figs. 6 and 7. At this time 25% of shoots and 20% of roots were simulated to be removed; gross photosynthesis 20 g m⁻² day⁻¹ and temperature 20°C.

The amount of $W_P + W_{ST}$ relative to top dry matter was simulated to vary between 11 and 33%. In the roots the W_{SR} pool varied between 2.5 and 11%. The lowest figures were obtained at the last day of the periods of low light and the highest values at the last day of the high light periods. These simulated results agreed quantitatively with experimentally obtained data of the content of water soluble carbohydrate of *Lolium* under varying light conditions (Deinum, 1966; Barta, 1975).

Simulation 2: Partitioning and utilization of assimilates

As the model was able to predict measured results of respiration and growth adequately the next step was to see how the model would predict partitioning of dry matter between shoots and roots. Cooper & Thornley (1976) showed that by increasing the root temperature of tomato plants, the root fraction of total dry matter decreased. At the low rate of photosynthesis vegetative plants have a higher shoot:root ratio than plants grown at higher level of photosynthesis (Robson & Lewis, 1968; Ryle 1970; Parsons & Robson, 1981).

At a constant temperature, 20°C, change of the photosynthesis in simulations showed, that the present model predicted the same results (Fig. 8).

Assuming a gross photosynthesis of 20 g CH₂O m⁻² day⁻¹ and a Q_{10} of 2 for all kinetic parameters, the shoot:root ratios were simulated at a constant shoot temperature (20°C) and varying root temperature (5–25°C) (Fig. 8). In the simulation the K_R was assumed to act in the shoots. Shoot:root ratio increased or the root fraction fell with increasing root temperature, in agreement with literature.

Brouwer (1966) and Fick et al. (1975) showed that if the shoot:root ratio was changed

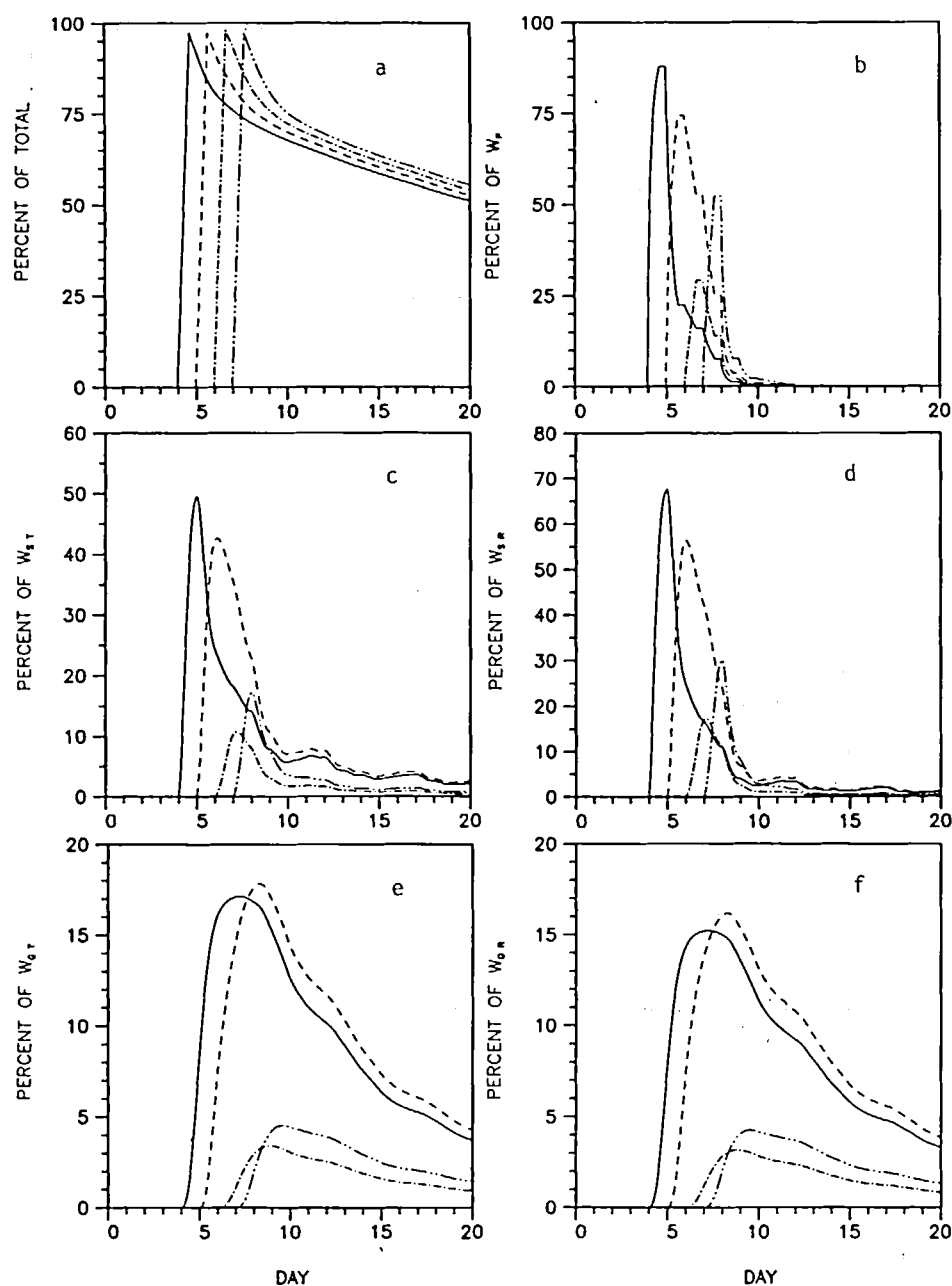


Fig. 10. Simulation of the retention of the carbon assimilated during selected days of the experiment shown in Fig. 6: day 5 (—), 6 (---), 7 (-·-·-), and 8 (····-). (a) relative to the total amount assimilated on the respective days; (b) the amount in the transport pool W_P , relative to the total amount in the pool; (c, d) the amounts in the storage pools of shoots (W_{sT}) and roots (W_{sR}) relative to the total amounts in the pools, respectively. (e, f) the amount in the structural pool of shoots (W_{GT}) and of roots (W_{GR}) relative to the total amount in the pools, respectively.

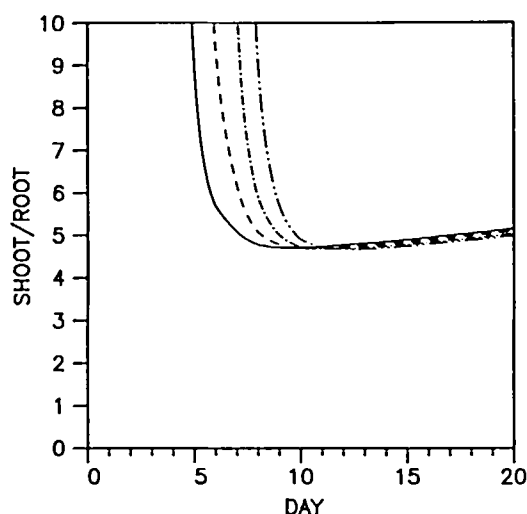


Fig. 11. The predicted time course of shoot: root ratio of the carbon assimilated on days 5–8 as given in Fig. 10, with same symbols.

by either partial defoliation or root pruning, the original ratio was restored during the subsequent growth. The present model predicts the same tendency (Fig. 9); after simulated defoliation or root pruning, the shoot:root ratio converges towards the original ratio.

Simulation 3: Predictions of carbon retention

As the behaviour of the model was in agreement with several experiments, it was then used for prediction of carbon retention in the five different pools. As initial conditions and as driving variable the experimental data of those presented in Fig. 6 were applied. The assimilated carbon of each of the days 5–8 was followed by simulation. The first two days, 5 and 6, were at high and the succeeding two days, 7 and 8, at low rates of photosynthesis. The carbon assimilated during each of the four days was followed in each of the pools W_P , W_{ST} , W_{GT} , W_{SR} , and W_{GR} , respectively, and thus labelled the carbon dynamics of the five pools were predicted for the succeeding period (Fig. 10a–f).

Independent of the rate of photosynthesis, the relative amount of retained labelled carbon fell and was after 15 days near half of the assimilated carbon, the other half was respired (Fig. 10a).

The predictions of the amounts of labelled carbon relative to the total amount of the pools W_P , W_{ST} , and W_{SR} , showed dependency on the size of photosynthesis of the day and that of the proceeding day. The latter effect was due to the time lag introduced by translocation and utilization.

In the transport pool, W_P , the carbon had the shortest residence time, and it had almost disappeared after four days (Fig. 10b). Due to the recirculation of degraded structural matter, the W_S pools would not be completely emptied, and the declining relative amount was depending on the amount assimilated (Figs. 10c, d). Carbon of structural materials was the most stable (Figs. 10e, f). The relative maximum amount of a one day assimilated carbon stored in structural materials was 18 and 5% in shoots and roots, respectively. Due to growth and degradation these relative amounts were halved after approximately 8 and 6 days.

Maximum structural dry matter for shoots and roots of labelled carbon was achieved 2.5 days after maximum amount in the W_P pool was reached. Shoot:root ratio of labelled carbon was initially infinite due to initial accumulation in W_P but declined to a minimum of 4.7 obtained after 4 days. Then due to the higher respiration loss of roots it gradually increased again (Fig. 11).

DISCUSSION

The model is a further development of Thornley's (1977) model as it considers also net partitioning, and take into account the different utilization efficiencies of shoots and roots. The basic assumption is that all kinetic involved are of first-order without direct feedbacks between sources and sinks.

The use of first-order kinetics for partitioning is principally not in agreement with the approach of Mason & Maskell (1928), who suggested that translocation is driven by concentration gradients between the regions. The model can, however, give an approximate solution which could be explained by a low concentration at the sink sites. By the method of parameter estimation, it was not possible to measure gross fluxes and it is a simplification only to regard net fluxes.

In estimating the parameters it was assumed that they did not change during the course of 48 h darkness and 48 h of light. This is an approximation. Hansen & Jensen (1977) found that Y_G for *Lolium multiflorum* declined when day/night periods were changed from 16/8 h to 8/16 h. The length of photoperiod for *Poa pratensis* influenced relative growth rates and shoot:root ratio (Heide et al., 1985). These experiments lasted, however, several weeks compared to the present treatments, where K_{GT} and K_{GR} were estimated after about 10 h and 20 h, respectively, and K_T and K_R after 48 h.

The assumption of a pool for transport, W_P , agrees with Ho (1976, 1978), and means that all soluble carbohydrate of the shoots should not be related to transport, or to shoot respiration.

The shoot:root dry matter ratios as simulated are in quantitative agreements with measured results from ryegrass (Hansen, 1978; Parsons & Robsons, 1981).

The ratio between the partitioning coefficients, $K_T:K_R=2.85$, was much smaller than the shoot:root dry matter ratio, due to the relative higher respiratory loss of the roots. This may be caused by the respiratory cost by uptake of ions (Hansen, 1979, Veen 1981) and/or by the alternative oxidative pathway (Lambers, 1979). The influence of different respiratory activity on the dry matter ratio between organs was also shown by Barnes (1979).

It is striking that the model in spite of the assumptions of a fixed relation between the partitioning parameters K_T and K_R agrees with the functional relation of Brouwer (1966). It expresses that: "shoot size \times shoot activity = root size \times root activity" (Davidson, 1969). As this relation was not used as a condition, the agreement is a result of the differences of efficiencies of carbon utilization and functions of shoots and roots. In the short term agreement may also be the case when nutrient uptake is limited, because root respiration then declines (Hansen, 1979; 1980).

The value of K_G in shoots is lower than that estimated by Barnes & Hole (1978), and their K_D value was higher for unculm barley. The present model has no compartments of non-degradable materials, as suggested by Thornley (1977). Assuming that his fraction is identical with the crude fibre fraction, this would then be 15–30% depending on age. As K_D , however, was estimated on the basis of the maintenance coefficient, obtained by relating respiration to growth and total organic dry matter, the maintenance coefficient should also be corrected for the non-degradable material. The shoot value of K_D is in reasonable agreement with the value estimated by Prosser & Farrar (1981). The K_D -values include the turnover of protein, which contributes considerably to maintenance respiration (Penning de Vries, 1975).

The present analysis makes use of the maintenance respiration as the cost of turnover of structural material alone. During darkness the amount of substrate and therefore respiration will decrease, and at a certain time depending on the amount of structural materials, the values of K_G , K_D , Y_G and the initial amount of substrate, maintenance of *status quo*

of the plants cannot be sustained. Respiration will continue to decrease beyond this point, but it is then smaller than maintenance respiration and senescence will occur (Thornley, 1977).

According to the model there is a linear relation between carbon of the storage pool and respiration. Some indication of this has been found (Challa, 1976; Farrar, 1980; Penning de Vries et al., 1979). However, such a relation is difficult to prove as a part of soluble carbohydrate found belonging to the transport pool.

The model has some similarities with the model of Prosser & Farrar (1981). Both models make use of first-order kinetics for which there is some experimental support, but this is also disputed (Farrar, 1981).

The model of Prosser & Farrar (1981) contains a storage pool of mainly starch and fructosans. The presence of such pools means time lags and these effects are implicit in the parameter values of the present model.

By this model some of the dynamics of the shoot:root ratio may have been explained due to the differences in utilization of carbon for growth and maintenance. Events affecting respiration will influence the shoot:root ratio. The model can be further developed, for example for study of the influence of limited nutrient supplies.

ACKNOWLEDGEMENTS

We thank Professor M. Flensted-Jensen, Department of Mathematics, the Royal Veterinary and Agricultural University, for critically reading the manuscript and Mrs Ester Rasmussen for her help in the preparation of the manuscript.

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APPENDIX

I. Symbols of state variables to the model

(here given per area, but could also be per pot as used in the experiments).

- W_P = pool of recently assimilated carbohydrates, g $\text{CH}_2\text{O m}^{-2}$
- W_{ST}, W_{SR} = storage pools for shoots (T) and roots (R)
- W_{GT}, W_{GR} = structural dry matter for shoots (T) and roots (R), $\text{CH}_2\text{O m}^{-2}$

II. Kinetic parameters of the model

- K_T, K_R = first order rate constants for partitioning assimilates to shoots (T) and roots (R), day^{-1}
- K_{GT}, K_{GR} = first order rate constants of mobilizing carbon from the storage pools in shoots (T) and roots (R), day^{-1}
- K_{DT}, K_{DR} = first order rate constants of degradation of structural materials in shoots (T) and roots (R), day^{-1}
- Y_{GT}, Y_{GR} = efficiencies of conversion carbon into structural materials, for shoots (T) and roots (R)
- M_T, M_R = coefficients of maintenance respiration, day^{-1}
- R_T, R_R = shoots (T) and roots (R) respiration rates, g $\text{CH}_2\text{O m}^{-2} \text{ day}^{-1}$
- P_G = gross photosynthesis (= CO_2 -uptake + R_T in light) g $\text{CH}_2\text{O m}^{-2} \text{ day}^{-1}$