

# Simulating the partitioning of biomass and nitrogen between roots and shoot in crop and grass plants

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Received 4 September 2003; accepted 23 March 2004

## Abstract

Quantification of the assimilate partitioning between roots and shoot has been one of the components that need improvement in crop growth models. In this study we derived two equations for root-shoot partitioning of biomass and nitrogen (N) that hold for crops grown under steady-state conditions. The equations are based on the concept of the functional balance between N uptake by roots and carbon fixation by shoots, and incorporate the assumption that plants control their root-shoot partitioning in order to maximize relative growth rate. The equations do not have their own parameters but use several variables as inputs that can be calculated from sub-models for root N uptake and shoot carbon fixation in a general plant growth model. Given reports from the literature that the partitioning models – if expressed as a function of plant-N status – might be suitable for steady-state as well as non-steady-state conditions, our equations were deliberately applied to non-steady-state conditions. The predicted crop root-shoot partitioning and its responses to radiation, water and N agreed qualitatively with the expected trends. The predicted response to elevated carbon dioxide varied and depended on the timing and amount of N applied. Quantitative tests with data from root and shoot pruning experiments with grass plants carried out by others showed that model predictions also agreed with observed root-shoot ratios, suggesting that our equations provided a valuable semi-mechanistic approach to the prediction of root-shoot relationships under any growth conditions.

*Additional keywords:* allocation, functional equilibrium, root-shoot ratio, grass, wheat

## Introduction

The partitioning of assimilates between roots and shoot is important for process-based

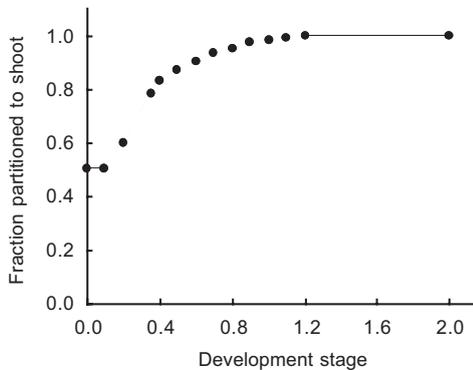


Figure 1. Fraction of newly formed biomass partitioned to the shoot in wheat, in relation to development stage (stage 0 = emergence; stage 1 = flowering; stage 2 = maturity). Pattern according to the SUCROS crop growth model (Goudriaan & Van Laar, 1994).

modelling of plant growth. It is the major partitioning process in models for grass growth. For arable crops, modellers usually describe the partitioning in two steps: first, between roots and shoot, and then within shoot organs to account for the growth of grains or seeds (Goudriaan & Van Laar, 1994). Highly empirical approaches have been used to describe root-shoot partitioning, such as specific experiments to derive partitioning coefficients as a function of development stage (Figure 1), or fitting allometric formula to the data (e.g. Troughton, 1977). More physiologically based approaches for root-shoot relationships are the functional balance theory and the transport-resistance mechanism.

The transport-resistance approach (Thornley, 1972) describes two substrates, carbon (C) and nitrogen (N), and assumes that their transport rate is proportional to root-shoot substrate concentration gradients divided by a transport resistance. The partitioning is a result of transport and chemical conversion occurring in the roots and shoot. The overall framework of this model is mechanistic and most of the available evidence on the root-shoot ratio is compatible with its prediction (Wilson, 1988). The way to define underlying resistances is empirical, using resistance coefficients scaled by structural mass with an allometric constant. Reynolds & Thornley (1982), Johnson (1985) and Johnson & Thornley (1987) abandoned the transport-resistance hypothesis and instead introduced a 'partitioning function' in which partitioning was assumed to be a function of the C-N ratio of substrate pools. Validation of all of these models requires information on the dynamics of C and N substrates in both roots and shoot. This information is not readily predicted, nor amenable to experimental measurement (Charles-Edwards, 1976; Brouwer, 1983).

The functional-balance concept has already been proposed several decades ago (e.g. Brouwer, 1962). Davidson (1969) extended the concept to predict the root-shoot ratio by suggesting a quantitative proportionality between the activity of the roots (which supply N) and the activity of the shoot (which supplies C). While no attempt was made

to define the causal mechanism for the proportionality, the approach is appealing because of its simplicity. However, the functional balance theory does not predict any optimal performance of plants during acclimatization to their growth environment (Hilbert, 1990). Because plants are plastic in adjusting the distribution between organ systems in response to external resource limitations, growth maximization is amongst the criteria used to derive partitioning models (Gleeson, 1993; Kleemola *et al.*, 1996). One assumption used to model partitioning is that plants optimize their behaviour by maximizing relative growth rate (RGR) (Kachi & Rorison, 1989; Ågren & Franklin, 2003). This assumption was also proven experimentally (Van Der Werf *et al.*, 1993b).

The functional balance theory applies to steady-state plant growth, which refers to the early growth of plants when exposed to a constant environment at an exponential rate while maintaining a constant chemical composition (Charles-Edwards, 1976). Several studies indicate that partitioning models for steady-state plant growth could also be applied to non-steady-state conditions. Hirose (1986) and Hirose *et al.* (1988) highlighted a crucial role of whole-plant N in controlling partitioning, in both steady-state and non-steady-state conditions. Ågren & Ingestad (1987) presented a similar argument, using a phenomenological model to understand root-shoot ratio in relation to plant-N status. Experimental data of Van Der Werf *et al.* (1993a), De Pinheiro Henriques & Marcelis (2000) and De Groot *et al.* (2002) indicate that partitioning of both C and N is consistently related to the internal-N status for plants under all conditions. Van Der Werf *et al.* (1993a) concluded that the partitioning functions, once expressed in relation to internal plant-N status, are general for both steady-state and non-steady-state conditions. They also expressed a common view of many modellers: the need for simple general partitioning functions for plant growth modelling.

The objective of our study was to derive two simple equations for the root-shoot partitioning of new biomass and N that can be readily applied to many plant growth models. The equations were based on a functional balance theory for steady-state conditions, and included the optimal allocation mechanism for a maximized RGR. Given the conclusion of Van Der Werf *et al.* (1993a) that the partitioning models if expressed as a function of plant-N status might be suitable for steady-state and non-steady-state conditions, our equations were deliberately applied to non-steady-state conditions. They were first tested qualitatively to the whole-season growth of wheat (*Triticum aestivum*) in terms of the partitioning responses to radiation, N, water and carbon dioxide (CO<sub>2</sub>), i.e., environmental factors expected to modulate the root-shoot ratio (Wilson, 1988). Next, quantitative evaluation of the models was performed using data from the literature on partitioning in response to leaf and root pruning in grass plants.

## Materials and methods

### Models

All model symbols, with definitions and dimensions are listed in Table 1 and Appendix 2.

Table 1. List of symbols used in the partitioning model of Yin *et al.* (2001).

Symbol	Definition, dimension and algorithm
$f_C$	Fraction of carbon in newly formed biomass, g C per g dry weight, 0.476
$f_N$	Fraction of N in newly formed biomass, g N per g dry weight, $(\Delta N / \Delta t) / (\Delta W / \Delta t)$
$F_N$	Fraction of N in biomass, g N per g dry weight, $(N_R + N_S) / (W_R + W_S)$
$N_R$	Root N, g N per m <sup>2</sup> ground, state variable with its rate as $\Delta N_R / \Delta t$
$N_S$	Shoot N, g N per m <sup>2</sup> ground, state variable with its rate as $\Delta N_S / \Delta t$
$W_R$	Root biomass, g dry weight per m <sup>2</sup> ground, state variable with its rate as $\Delta W_R / \Delta t$
$W_S$	Shoot biomass, g dry weight per m <sup>2</sup> ground, state variable with its rate as $\Delta W_S / \Delta t$
$\lambda_{w,s}$	Fraction of newly formed biomass partitioned to shoot
$\lambda_{n,s}$	Fraction of newly absorbed N partitioned to shoot
$\sigma_C$	Specific shoot activity, g C per g dry weight per day
$\sigma_N$	Specific root activity, g N per g dry weight per day
$\sigma_C$	Specific shoot activity, g C per g N per day
$\sigma_N$	Specific root activity, g N per g N per day
$\Delta C / \Delta t$	Net rate of shoot C fixation, g C per m <sup>2</sup> ground per day, 0.6 $P_C$
$\Delta N / \Delta t$	Rate of root N uptake, g N per m <sup>2</sup> ground per day, $\min(n_{sup}, n_{dem})$
$\Delta N_R / \Delta t$	Increment of root biomass, g dry weight per m <sup>2</sup> ground per day, $(1 - \lambda_{n,s})\Delta N / \Delta t - F_{N,Rmin}\chi W_R$
$\Delta N_S / \Delta t$	Increment of shoot biomass, g dry weight per m <sup>2</sup> ground per day, $\lambda_{n,s}\Delta N / \Delta t - n_{bSla}r_{s,LV}$
$\Delta W / \Delta t$	Increment of total biomass, g dry weight per m <sup>2</sup> ground per day, $(\Delta C / \Delta t) / f_C$
$\Delta W_R / \Delta t$	Increment of root biomass, g dry weight per m <sup>2</sup> ground per day, $(1 - \lambda_{w,s})\Delta W / \Delta t - \chi W_R$
$\Delta W_S / \Delta t$	Increment of shoot biomass, g dry weight per m <sup>2</sup> ground per day, $\lambda_{w,s}\Delta W / \Delta t - r_{s,LV}$

*Equation for biomass partitioning between roots and shoot*

The derivation by Charles-Edwards (1976), re-presented in Appendix 1, has shown that the following holds for spaced plants under steady-state conditions:

$$\Delta W / \Delta t = (\Delta W_s / \Delta t)(f_C\sigma_N + f_N\sigma_C) / f_C\sigma_N \tag{1}$$

where  $\sigma_N$  and  $\sigma_C$  are specific root and shoot activities, respectively, defined as:

$$\sigma_N = (\Delta N / \Delta t) / W_R \tag{2a}$$

$$\sigma_C = (\Delta C / \Delta t) / W_S \tag{2b}$$

The fraction of newly formed plant biomass partitioned to the shoot,  $\lambda_{w,s}$ , can be derived from Equation 1 as:

$$\lambda_{w,s} = \frac{\Delta W_s}{\Delta W} = \frac{1}{1 + f_N\sigma_C / f_C\sigma_N} \tag{3a}$$

Substituting  $\sigma_N$  and  $\sigma_C$  from Equations 2a and 2b into Equation 3a gives:

$$\lambda_{w,s} = \frac{1}{1 + f_N W_R \Delta C / f_C W_S \Delta N} \quad (3b)$$

Equations 3a and 3b do not account for any control mechanism for partitioning that may have emerged from evolutionary selection pressure. There is evidence that mechanisms that control shoot-root ratios have evolved to maximize RGR (Johnson & Thornley, 1987; Van Der Werf *et al.*, 1993a, b). The analysis by Hilbert (1990) for steady-state exponential growth has shown that in order to achieve optimum plant-N content and its associated root-shoot ratio that maximize RGR,  $\sigma_N$  and  $\sigma_C$  have to be balanced as (Hilbert's Equation A7):

$$\sigma_N = \sigma_C^2 / (f_C \cdot d\sigma_C / dF_N) \quad (4)$$

Substituting Equation 4 into Equation 3a gives a model of root-shoot biomass partitioning with a maximized RGR:

$$\lambda_{w,s} = \frac{1}{1 + f_N / \sigma_C \cdot d\sigma_C / dF_N} \quad (5)$$

*Equation for nitrogen partitioning between roots and shoot*

From a similar logic as for biomass, the fraction of newly absorbed N partitioned to the shoot,  $\lambda_{N,s}$ , can be formulated as:

$$\lambda_{N,s} = \frac{1}{1 + f_N \sigma_C / f_C \sigma_N} \quad (6a)$$

$$\lambda_{N,s} = \frac{1}{1 + f_N N_R \Delta C / f_C N_S \Delta N} \quad (6b)$$

In such a case, specific root and shoot activities ( $\sigma_N$  and  $\sigma_C$ ) are defined as:

$$\sigma_N = (\Delta N / \Delta t) / N_R \quad (7a)$$

$$\sigma_C = (\Delta C / \Delta t) / N_S \quad (7b)$$

To apply the equation for a maximized RGR to the N-partitioning model,  $\Delta C$  and  $\Delta N$  from Equation 2 are substituted into Equation 6b, which results in:

$$\lambda_{N,s} = \frac{1}{1 + f_N \sigma_C N_R W_S / f_C \sigma_N N_S W_R} \quad (8)$$

Substituting Equation 4 into Equation 8 gives an equation for root-shoot N partitioning:

$$\lambda_{N,S} = \frac{I}{I + [f_N N_R W_S / (\sigma_N N_S W_R)] \cdot d\sigma_C / dF_N} \quad (9)$$

*A general model routine for implementing the partitioning equations*

Equation 5 uses three input variables ( $\sigma_C$ ,  $f_N$ , and  $d\sigma_C/dF_N$ ) and Equation 9 needs additional inputs for  $W_S$ ,  $W_R$ ,  $N_S$  and  $N_R$ .  $\sigma_C$  was calculated by definition (Equation 2b). The term  $d\sigma_C/dF_N$  was numerically given by:

$$d\sigma_C/dF_N = [\sigma_{C(F_N + \Delta F_N)} - \sigma_{C(F_N)}] / \Delta F_N \quad (10)$$

where  $\Delta F_N$  is a small  $F_N$  increment (set at  $0.001F_N$ );  $\sigma_{C(F_N + \Delta F_N)}$  and  $\sigma_{C(F_N)}$  are specific shoot activities when plant-N content is  $(F_N + \Delta F_N)$  and  $F_N$ , respectively, which were also estimated on the basis of Equation 2b. A general model that contains components for root N uptake and for shoot C fixation can be used for further calculations. Here we used a daily time-step model of Yin *et al.* (2001) in which  $W_S$ ,  $W_R$ ,  $N_S$  and  $N_R$  are state variables. Their rate equations are given in Table 1. Further model details are summarized in Appendix 2.

### Model evaluation for wheat and grass

Wheat was chosen to qualitatively assess model behaviour for an arable crop. Simulations were run from seedling emergence to crop maturity. The initial values of  $W_S$  and  $W_R$  were determined from seeding rate and seed weight, assuming 35% germination and a standard initial root-shoot ratio of 1.0 (Goudriaan & Van Laar, 1994). Initial  $N_S$  and  $N_R$  were determined assuming 5% shoot-N at emergence and a  $N_R:N_S$  ratio as given by Kachi & Rorison (1989). Simulations were carried out, first for constant and next for seasonally varying environmental conditions. The value for the constant-environment to show the basic partitioning pattern was set at:  $I_C = 15$ ,  $T = 15$ ,  $n_{sup} = 0.8$ ,  $w_{sup} = 4$ ,  $C_a = 350$ ,  $e_a = 1.5$ ,  $u = 2$ ,  $D = 50,400$  (see Appendix 2 for definition). The values for  $I_C$ ,  $n_{sup}$ ,  $w_{sup}$  and  $C_a$  were then changed, each to an extent to illustrate the response of partitioning to these variables under constant environmental conditions. The response to various scenarios in N supply, water supply and CO<sub>2</sub> levels under seasonally varying environments was examined using 1993 weather data for Wageningen (52°N). The starting time of simulation was set at the 90th day of the year. The use of actual weather data provides a more relevant illustration of partitioning models in predicting responses to environmental variables encountered by plants in the field (Hunt *et al.*, 1998).

Next, our equations were quantitatively assessed for predicting the response of grass plants to pruning, using data from two experiments (Schapendonk *et al.*, 1997; Van Loo *et al.*, 1992). For both data sets, the version for grass of the same model (Yin *et al.*, 2001) was used. Initial values of the state variables were set at the measured

values. In the experiment of Schapendonk *et al.* (1997), grass (*Lolium perenne*) swards grown for two years (1994–1995) in the Wageningen Rhizolab were cut ten times per year at intervals of 20 to 24 days. After each cut, N was applied at a rate of 8 g m<sup>-2</sup>. From these individual cuts, the value of root-shoot biomass partitioning was derived. In the experiment of Van Loo *et al.* (1992), six grass populations (three diploids and three tetraploids of *Lolium perenne*) were grown in a greenhouse in 1989. Two steady-state N supply conditions were used to achieve a shoot-N content of 0.045 or 0.0225 g N per g dry matter. Root-shoot ratios for both biomass and N were measured by trimming leaves and roots at intervals of four weeks. The lower N treatment resulted in the highest root-shoot ratio.

## Results and discussion

### Basic form of partitioning pattern in wheat

The simulated fraction partitioned to the shoot and the root-shoot ratio for wheat as a function of development stage ( $S$ ), using constant-environment values and 1.0 as the initial root-shoot ratio, are presented in Figure 2. The root-shoot ratio remained constant until  $S$  reached 0.3, 15 days from emergence (DFE), resulting in a fixed-partitioning period. After that, biomass was increasingly partitioned to the shoot. The

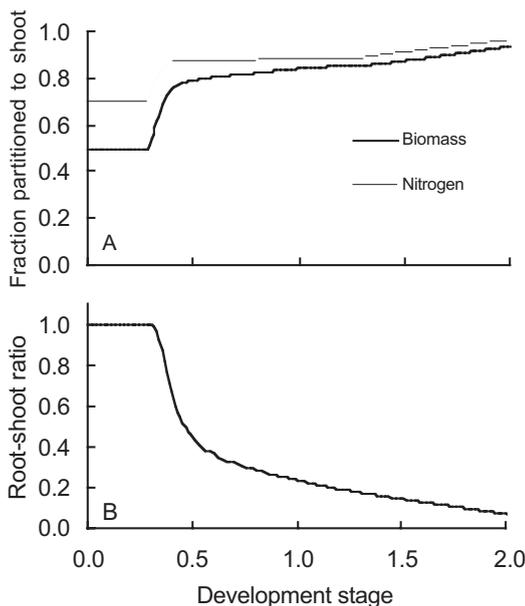


Figure 2. Simulated fraction of newly formed biomass and N partitioned to the shoot (A), and the root-shoot ratio (B) in wheat, in relation to development stage. Development stages as defined in Figure 1.

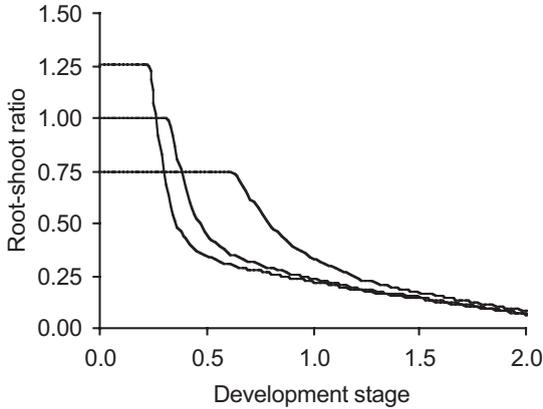


Figure 3. Simulated root-shoot ratio in wheat, in relation to development stage for three different initial root-shoot ratios (0.75, 1.00 and 1.25). Development stages as defined in Figure 1.

length of the fixed-partitioning period decreased with increasing initial root-shoot ratio, but the root-shoot ratio at crop maturity appeared to be only slightly affected by the initial value (Figure 3).

Also the N partitioning during the early growth period could be predicted from the initial root-shoot ratio. Its pattern was similar, with only a slightly higher value than that of biomass partitioning (Figure 2A), which agrees with experimental observations of Van Der Werf *et al.* (1993a) and De Pinheiro Henriques & Marcelis (2000). For this reason, the N partitioning results, unless specified otherwise, are no longer shown in the figures.

The modelled partitioning pattern as a function of  $S$  (Figure 2A) was similar to the experimentally derived one (Figure 1). The simulated fraction allocated to the shoot was equal to the actual shoot fraction of biomass in very young plants, which has also been simulated by Thornley (1998). This result of our simulation can be mathematically explained from the fact that early N uptake is determined by crop-N demand ( $n_{\text{dem}}$ ) and as a consequence, the value of  $f_N$  can be computed as:  $f_N = n_{\text{dem}} / (\Delta W / \Delta t)$ . Substituting Equation 1.1 in Appendix 1 and the  $n_{\text{dem}}$  equation in Appendix 2 gives:  $f_N = W_R \sigma_C / (W_S d\sigma_C / dF_N)$ , which means that Equations 5 and 9 predict the root-shoot ratio as the initially set value. Clearly, the simulated partitioning pattern depends on sub-models for estimating plant N uptake and canopy C fixation, which largely determine  $f_N$  and  $d\sigma_C / dF_N$ , respectively.

### Effects of constant environments on root-shoot partitioning in wheat

The response of wheat root-shoot partitioning to a change in environmental conditions is given in Figure 4. The response to a 50% change in radiation (Figure 4A) and in N supply (Figure 4B) was as expected, i.e., high radiation and low N resulted in a preferential partitioning to roots (Brouwer, 1983; Wilson, 1988). An increased partitioning to roots in response to a 50% decrease in water supply (Figure 4C) was also expected, but

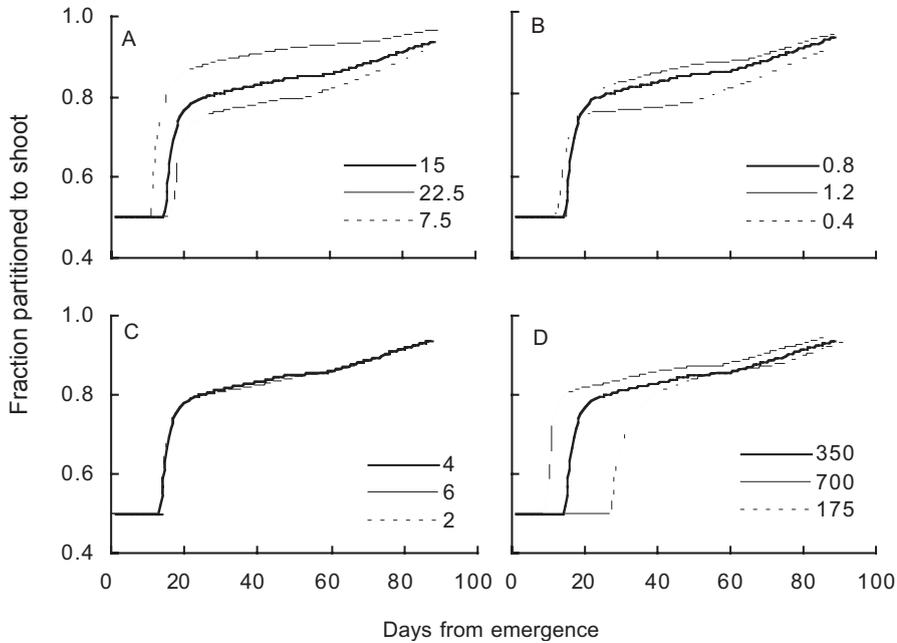


Figure 4. Simulated partitioning of newly formed biomass in wheat in response to radiation (7.5, 15 or 22.5 MJ m<sup>-2</sup> day<sup>-1</sup>; A), N supply (0.4, 0.8 or 1.2 g N m<sup>-2</sup> day<sup>-1</sup>; B), water supply (2, 4 or 6 mm day<sup>-1</sup>; C) and atmospheric CO<sub>2</sub> (175, 350 or 700 μmol mol<sup>-1</sup>; D). The thin and thick uninterrupted lines in C overlap because identical simulation results were obtained with 4 and 6 mm water day<sup>-1</sup>.

the effect was only small because the standard water supply value for simulation was high and a 50% decrease did not yield water stress. The high water supply value was deliberately chosen to avoid any confounding effect of water stress on the predicted basic partitioning pattern (a clearer effect of water stress will be illustrated later). Doubling the CO<sub>2</sub> level increased the fraction partitioned to the shoot (Figure 4D). A changed CO<sub>2</sub> level had a strong effect on the timing of the end of the fixed-partitioning period. The simulated effect of CO<sub>2</sub> levels on root-shoot ratios will be discussed later.

### Effects of varying environments on root-shoot partitioning in wheat

The simulated partitioning patterns using actual weather data for Wageningen are presented in Figures 5–7. After the initial period of fixed partitioning, the partitioning fraction fluctuated in response to the varying environments.

The effect on partitioning of an application of 20 g N m<sup>-2</sup> and its timing, in comparison with no N applied, is shown in Figure 5. The additional N applied at 0 DFE or 20 DFE increased the shoot fraction. However, before this general effect became apparent, the N application first caused a reduced shoot fraction for some days. This phenomenon was most pronounced in the simulation with N applied at 20 DFE.

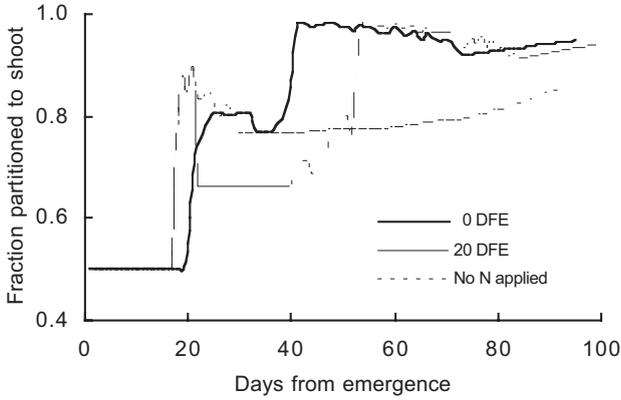


Figure 5. Simulated partitioning of newly formed biomass in wheat without drought stress, under conditions with indigenous soil-N supply only (i.e., no N applied) or with 20 g N m<sup>-2</sup> (uninterrupted lines) applied at 0 or 20 days from emergence (DFE).

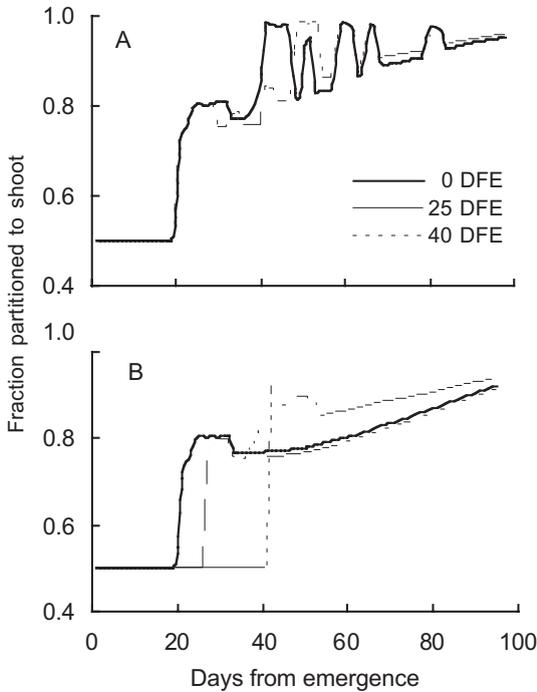


Figure 6. Simulated partitioning of newly formed biomass in wheat, in response to an application of 50 mm water at 0, 25 or 40 days from emergence (DFE). Simulations were carried out using weather data including rainfall (A), or excluding rainfall (B). The thin and thick uninterrupted lines in A overlap because identical simulation results were obtained with water applied at 0 and 25 DFE.

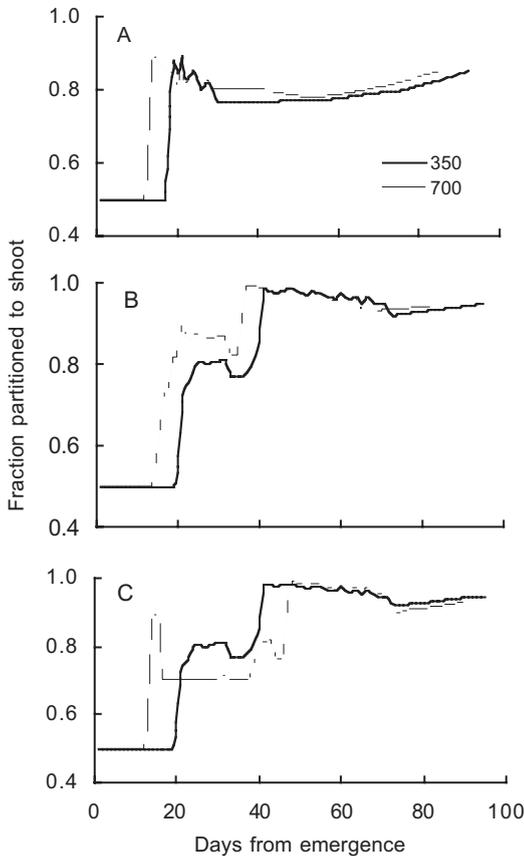


Figure 7. Simulated partitioning of newly formed biomass in wheat, in response to doubled atmospheric  $\text{CO}_2$  (350 versus 700  $\mu\text{mol mol}^{-1}$ ) under the conditions of no N applied (A), 20  $\text{g N m}^{-2}$  applied at emergence (B), and 20  $\text{g N m}^{-2}$  applied 15 days from emergence (C).

The timing of an application of 50 mm water had only a small effect on partitioning (Figure 6A), because an adequate soil moisture level was maintained by natural rainfall. When rainfall was excluded to simulate drought, the response to an application of 50 mm water was strong and swift, with a high shoot fraction promoted by the wet conditions (Figure 6B). The positive effect of water supply on shoot fraction is illustrated by comparing Figures 6A and 6B.

The predicted response to doubling the  $\text{CO}_2$  level interacted with the amount and timing of N supplies (Figure 7). For the crop with only indigenous soil-N supply, doubling the  $\text{CO}_2$  level led to a shorter fixed-partitioning phase (Figure 7A). When an additional 20  $\text{g N m}^{-2}$  was applied at emergence, a higher shoot fraction was predicted at 700 than at 350  $\mu\text{mol CO}_2 \text{ mol}^{-1}$  (Figure 7B). However, the opposite effect of doubling the  $\text{CO}_2$  level was observed, at least for some period, when the N was applied at 15 DFE (Figure 7C).

The above, simulated responses of root-shoot partitioning to radiation, water and N supplies were consistent with those observed in other plants (Brouwer, 1983; Wilson, 1988). Whether or not our model correctly predicted the response to CO<sub>2</sub> cannot be concluded with certainty. CO<sub>2</sub> was expected to affect root-shoot partitioning in the same direction as radiation does, since both are above-ground resources that stimulate photosynthesis (Wilson, 1988). In line with the results of Hilbert *et al.* (1991) and Friedlingstein *et al.* (1999), however, our simulation showed that under constant-environment conditions, the response to CO<sub>2</sub> was opposite to the response to radiation (Figure 4). If CO<sub>2</sub> was allowed to vary in combination with N supply, the effect of an elevated CO<sub>2</sub> level would not be consistent, but would depend on N-supply regimes (Figure 7). A literature survey (Arp, 1991; Luo *et al.*, 1994; Rogers *et al.*, 1996; Poorter & Nagel, 2000) learned that experimentally observed root-shoot ratios in response to elevated CO<sub>2</sub> levels were extremely variable (increase, no effect, decrease), and appeared to depend on soil N availability. This inconsistency probably reflects the possibility that many experimentally observed root-shoot ratios may be influenced by plant-N status, as plants grown under elevated-CO<sub>2</sub> conditions inevitably appear to have a lower plant-N content (Geiger *et al.*, 1999). Gunn *et al.* (1999), Bernacchi *et al.* (2000) and Harmens *et al.* (2000) indicated that partitioning is little affected if CO<sub>2</sub> is the only factor that varies provided the size of the plant is taken into account.

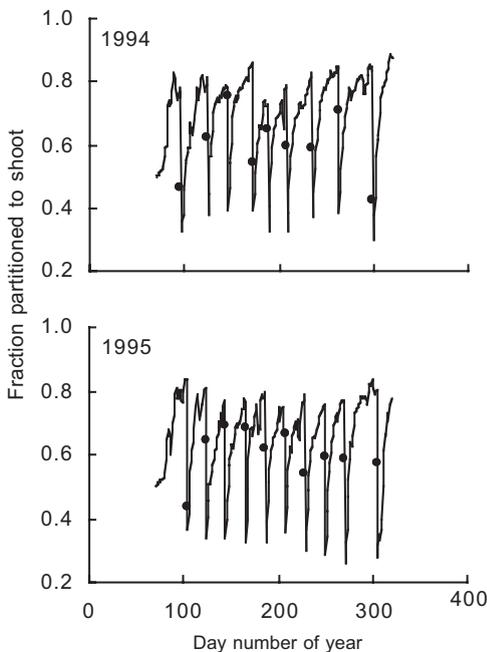


Figure 8. Simulated partitioning of newly formed biomass in grasses grown in 1994 and 1995 in Wageningen Rhizolab (curves), and the biomass partitioning (points) as observed by Schapendonk *et al.* (1997) on the basis of consecutive sampling. The sharp declines in the predicted fraction correspond to days when the grass was defoliated.

### Effect of pruning on shoot-root partitioning in grass

For the grass experiment of Schapendonk *et al.* (1997), where shoots were cut several times during the growth cycle, the model predicted a transient reduction in the shoot partitioning function after each cutting (Figure 8), which was similar to that predicted by the transport-resistance model (Thornley, 1998). Next, plants were simulated to switch rapidly to a distribution in favour of shoots. The modelled biomass partitioning agreed with the measured pattern based on ten samplings per year (Figure 8).

For the grass experiment of Van Loo *et al.* (1992), root-shoot ratios were calculated for each harvest, using trimmed root and shoot materials. Our approach adequately simulated variation of the root-shoot ratio for both biomass and N (Figure 9) obtained for various cutting times and N manipulations.

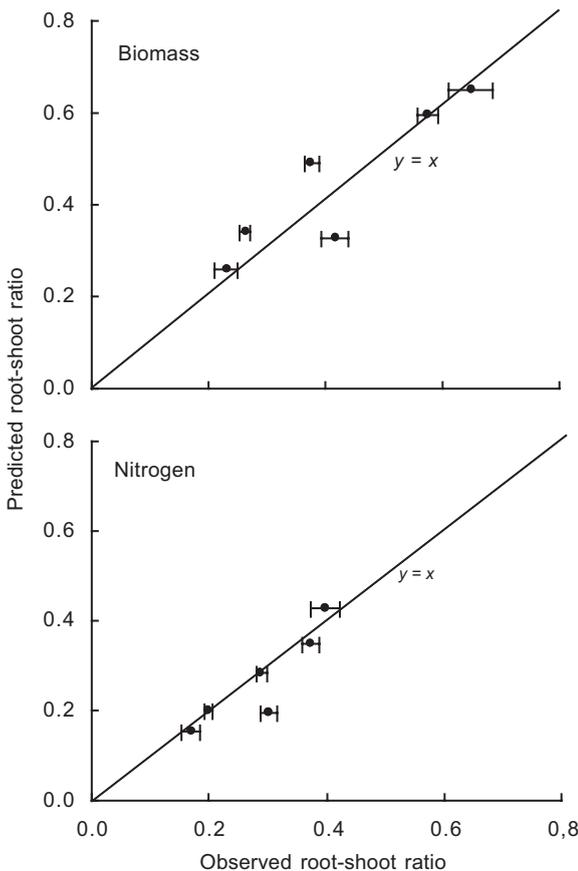


Figure 9. Comparison of simulated and observed root-shoot ratios of biomass and nitrogen for grasses grown in the greenhouse experiment of Van Loo *et al.* (1992). The observed values refer to the means of 6 grass populations. Bars = standard errors.

## Concluding remarks

Neither the mechanistic substrate-based transport-resistance model of Thornley (1972) nor its derivatives (Reynolds & Thornley, 1982; Johnson, 1985; Johnson & Thornley, 1987) have been widely used by the crop modelling community, probably because the C and N substrate levels cannot be easily measured or they are not simulated explicitly in many crop growth models. We aimed here to present simple equations, by combining the balanced root-shoot activity equation of Charles-Edwards (1976) and the conclusion of Hilbert (1990) that an optimum root-shoot ratio is required to maximize RGR. Our equations are valid under conditions of steady-state growth, because underlying equations of Charles-Edwards (1976) (i.e., equation 1) and of Hilbert (1990) (i.e., equation 4) only hold for steady-state plant growth. The equations cannot be mathematically justified for non-steady state conditions. Because of incorporating the formula for maximized RGR, our equations may not always reflect a pattern compatible with the classical functional-balance approach. One criticism could be that because of including terms for senescence occurring at stages towards maturity, equations for the increment of the state variables  $W_S$ ,  $W_R$ ,  $N_S$  and  $N_R$  in any model for non-steady state growth do not agree with those for newly formed biomass and N in our derivation. However, the simulated partitioning pattern changed little if senescence terms were left out (results not shown), indicating that our model simulates well an experimental observation of Gedroc *et al.* (1996) that partitioning in later growth stages is highly ontogenetically constrained. Our simulation showed a remarkable fit with experimental results found in the literature for grass plants under varying environmental conditions (Figures 8–9). This supports the conclusion of Van Der Werf *et al.* (1993a) that partitioning functions, once related to internal plant-N status, might be suitable for steady-state as well as non-steady-state conditions. Our equations do not require the estimation of empirical parameters. They cope with interactive effects of major environmental factors, thereby providing a valuable semi-mechanistic approach to modelling of partitioning for non-steady-state conditions in a general framework for predicting crop growth and ecosystem productivity.

## Acknowledgements

This work was supported by the European Commission's Environment & Change Programme through the MAGEC (Modelling Agroecosystems under Global Environmental Change) project (EU Contract ENV4-CT97-0693) carried out by Plant Research International, Wageningen. We thank Dr E.N. Van Loo for providing the climatic data from his greenhouse grass experiment.

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## Appendix 1

### Derivation of Equation 1 by Charles-Edwards (1976).

The proportionality between root and shoot functions, assumed in the functional balance approach, was formulated by Charles-Edwards (1976) as:

$$W_R \sigma_N / f_N = W_S \sigma_C / f_C = \Delta W / \Delta t \quad (1.1)$$

where

- $W_R$  = root biomass, g dry weight per m<sup>2</sup> ground;
- $W_S$  = shoot biomass, g dry weight per m<sup>2</sup> ground;
- $\sigma_N$  = specific root activity, g C per g dry weight per day;
- $\sigma_C$  = specific shoot weight, g N per g dry weight per day;
- $f_N$  = fraction of N in newly formed biomass, g N per g dry weight;
- $f_C$  = fraction of C in newly formed biomass, g C per g dry weight;
- $\Delta W / \Delta t$  = increment of total biomass, g dry weight per m<sup>2</sup> ground per day.

Note that, like in many studies using the functional balance approach, Charles-Edwards (1976) referred to  $f_N$  and  $f_C$  as the overall elemental fraction of plant biomass for the case of steady-state exponential growth. We, however, refer to these symbols as elemental fractions of newly formed plant biomass. This allows Equation 1.1 to be an identity, not only for steady-state growth, but also for non-steady-state conditions.

Provided that the specific root and shoot activities are independent of the root and shoot weights – which is a reasonable assumption for spaced plants under steady-state conditions – the following equation can be obtained by differentiating Equation 1.1 if  $f_N$ ,  $f_C$ ,  $\sigma_N$  and  $\sigma_C$  are taken to be constant:

$$(\sigma_N / f_N)(\Delta W_R / \Delta t) = (\sigma_C / f_C)(\Delta W_S / \Delta t) \quad (1.2)$$

The rate of change of total dry weight can then be written as:

$$\Delta W / \Delta t = \Delta W_R / \Delta t + \Delta W_S / \Delta t \quad (1.3)$$

Substituting  $\Delta W_R / \Delta t$  in Equation 1.2 into Equation 1.3 gives Equation 1.

## Appendix 2

### List of symbols with descriptions, units and algorithms in the model of Yin et al. (2001) for wheat and grass.

Symbol Definition, unit and algorithm

$C_a$	Atmospheric CO <sub>2</sub> concentration, μmol mol <sup>-1</sup> , input
$C_i$	Intercellular CO <sub>2</sub> concentration, μmol mol <sup>-1</sup> , $0.9 - 0.1D_a$
$D$	Daylength, s day <sup>-1</sup> , input
$D_a$	Vapour pressure deficit, kPa, $e_s - e_a$
$e_a$	Air vapour pressure, kPa, input
$e_s$	Saturation vapour pressure, kPa, $0.611e^{17.4T/(239+T)}$
$E_{ul}$	Upper leaf transpiration, mm water per m <sup>2</sup> leaf per day, $\min[kw_{sup} / (1 - e^{-kt}), E_{ul,p}]$
$E_{ul,p}$	Potential $E_{ul}$ , mm water per m <sup>2</sup> leaf per day, $[sR_n + 1200D_a / (r_{bh} + r_t)] / \{2.4 \cdot 10^6 [s + 0.067(r_{bw} + r_t + r_{s,p}) / (r_{bh} + r_t)]\}$
$F_{N,Rmin}$	Fraction of N in senesced roots, g N per g dry weight, 0.005
$H$	Plant height, m, 0.026L for grass, or as a logistic function set by 0.8 m for wheat
$I_G$	Incoming global radiation, MJ per m <sup>2</sup> ground per day, input
$I_o$	PAR incident upon uppermost leaves, MJ per m <sup>2</sup> ground per day, $0.5I_G$
$k$	Extinction coefficient of radiation in canopy, m <sup>2</sup> ground per m <sup>2</sup> leaf, 0.6
$k_n$	Extinction coefficient of leaf N in canopy, m <sup>2</sup> ground per m <sup>2</sup> leaf, 0.35
$K_{mC}$	Michaelis-Menten constant for CO <sub>2</sub> , μmol mol <sup>-1</sup> , $460e^{65800(T-25)/[298 \cdot 8.314(T+273)]}$
$K_{mO}$	Michaelis-Menten constant for O <sub>2</sub> , μmol mol <sup>-1</sup> , $330e^{1400(T-25)/[298 \cdot 8.314(T+273)]}$
$L$	Leaf area index (m <sup>2</sup> leaf per m <sup>2</sup> ground), state variable with rate = $s_{la}\lambda_{LV}\Delta W_s / \Delta t$
$L_N$	Leaf N-determined leaf area index, m <sup>2</sup> leaf per m <sup>2</sup> ground, $(1/k_n)\ln(1 + k_n N_{LV} / n_b)$
$n$	Upper-leaf N content, g N per m <sup>2</sup> leaf, $k_n N_{LV} / (1 - e^{-k_n L})$
$n_b$	Minimum leaf N content for photosynthesis, g N per m <sup>2</sup> leaf, 0.3
$n_{dem}$	Crop demand for N, g N per m <sup>2</sup> ground per day, $W_R \sigma_C^2 / (f_C \cdot d\sigma_C / dF_N)$
$n_{sup}$	Soil N supply, g N per m <sup>2</sup> ground per day, input
$N_{LV}$	Total leaf N content in canopy, g N per m <sup>2</sup> ground, = $N_s$ for grass or $N_s - 0.008W_{ST} - 0.0225W_{SD}$ for wheat
$p_{max}$	Light-saturated upper-leaf photosynthesis, g C per m <sup>2</sup> leaf per second, $V_{cmax} (C_i - \Gamma^*) / [C_i + K_{mC} (1 + 210 / K_{mO})]$
$P_C$	Canopy gross photosynthesis, g C per m <sup>2</sup> ground per day, $P_{ul} (1 - e^{-kL}) / k$
$P_{ul}$	Upper leaf photosynthesis, g C per m <sup>2</sup> leaf per day, $P_{ul,p} (1.6r_{s,p} + 1.3r_{bw} + r_t) / (1.6r_s + 1.3r_{bw} + r_t)$
$P_{ul,p}$	Potential $P_{ul}$ , g C per m <sup>2</sup> leaf per day, $\varepsilon p_{max} k I_o / (p_{max} + \varepsilon k I_o / D)$
$r_{bh}$	Upper-leaf boundary-layer resistance to heat, s m <sup>-1</sup> , $100\sqrt{w/u}$
$r_{bw}$	Upper-leaf boundary-layer resistance to water, s m <sup>-1</sup> , $0.93r_{bh}$
$r_s$	Upper-leaf stomatal resistance to water, s m <sup>-1</sup> , $(E_{ul,p} - E_{ul})[s(r_{bh} + r_t) + 0.067(r_{bw} + r_t)] / (0.067E_{ul}) + r_{s,p}E_{ul,p} / E_{ul}$
$r_{s,p}$	$r_s$ in the absence of drought stress, s m <sup>-1</sup> , $\{0.5363D(C_a - C_i) / [0.9P_{ul,p}(273 + T) - 1.3r_{bw} - r_t]\} / 1.6$
$r_t$	Turbulent resistance, s m <sup>-1</sup> , $0.74\{\ln[(2 - 0.7H) / (0.1H)]\}^2 / 0.16u$
$r_{s,LV}$	Rate of leaf senescence, g dry weight per m <sup>2</sup> ground per day, $[L - \min(L, L_N)] / (s_{la}\Delta t)$
$R_n$	Net radiation absorbed by upper leaf, J per m <sup>2</sup> leaf per day, $k(0.75I_G - R^{\uparrow})$

## Appendix 2 cont'd

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$R^{\uparrow}$	Outgoing long wave radiation, J per m <sup>2</sup> leaf per day, $5.67 \cdot 10^{-8} D(T + 273)^4 \max[0, 0.55(1 - e_a / e_s)]$
$s$	Slope of the $e_s$ - $T$ curve, kPa°C <sup>-1</sup> , $4158.6e_s / (T + 239)^2$
$S_{la}$	Specific leaf area, m <sup>2</sup> leaf per g leaf, 0.035
$S$	Development stage (dimensionless), a state variable with rate = $T/T_{sum}$
$T$	Temperature, °C, input
$T_{sum}$	Temperature sum requirement, °Cd, input constant
$u$	Wind speed, m s <sup>-1</sup> , input
$V_{cmax}$	Maximum upper-leaf carboxylation, g C per m <sup>2</sup> leaf per second, $V_{cmax25} e^{68000(T-25)/(298 \cdot 8.314(T+273))}$
$V_{cmax25}$	$V_{cmax}$ at 25°C, g C per m <sup>2</sup> leaf per second, $0.9644 \cdot 10^{-3}(n - n_b)$
$w$	Leaf blade width, m, 0.01 for wheat, 0.005 for grass
$w_{sup}$	Soil water supply for transpiration, mm per m <sup>2</sup> ground per day, input
$W_{SD}$	Seed mass, g dry weight per m <sup>2</sup> ground, a state variable with rate = $\lambda_{SD} \Delta W_S / \Delta t$
$W_{ST}$	Stem mass, g dry weight per m <sup>2</sup> ground, a state variable with rate = $(1 - \lambda_{LV} - \lambda_{SD}) \Delta W_S / \Delta t$
$\epsilon$	Quantum yield, g C per MJ, $54.72(C_i - \Gamma_*) / [2.1(4.5C_i + 10.5\Gamma_*)]$
$\lambda_{LV}$	Fraction of new shoot mass partitioned to leaves (dimensionless), $\min(0, 1-S)$
$\lambda_{SD}$	Fraction of new shoot mass partitioned to seeds (dimensionless), $\max\{0, \min[1, (S-1)/0.2]\}$
$\chi$	Relative root death rate, day <sup>-1</sup> , $\max(0, -0.02 + 0.035S)$ for wheat or $0.0015T$ for grass
$\Gamma_*$	CO <sub>2</sub> compensation point, $\mu\text{mol mol}^{-1}$ , $22.05K_{mC}/K_{mO}$