

Simulating the response of photosynthate partitioning during vegetative growth in winter wheat to environmental factors

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Abstract

Currently available models of photosynthate partitioning in crops are poorly developed compared to carbon and water balance models. This paper presents a dynamic photosynthate partitioning model (PPModel) that simulates the partitioning of crop biomass to leaf, stem and root through the interaction between carbon gain (assimilation less respiration) and transpiration, in relation to environmental factors. The central concept is the theory of plant functional equilibrium, in which transpirational loss and water uptake are balanced, within acceptable limits, by a dynamic partitioning of assimilates between shoot and root growth. The model was shown to perform effectively against experimental data for growth and partitioning of biomass in winter wheat (collected over a 2-year period), when environmental factors varied daily and water supply was controlled over a wide range.

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1. Introduction

Currently available models of photosynthate partitioning in crops are poorly developed due to an inadequate understanding of the partitioning process (Wardlaw, 1990).

Penning de Vries and van Laar (1982), Wilson (1988) and Supit et al. (1994) used empirical approaches to describe the partitioning of photosynthate to different plant organs. Empirical models assume different predetermined coefficients for each plant organ, while the effects of environmental factors are often not considered, although the coefficients might be empirical functions of environmental factors (Williams et al., 1989; Hoogenboom et al., 1992). These empirical approaches, providing a simple description of assimilate partitioning, are the ones generally used in crop growth models (Penning de Vries and van Laar, 1982; Marcelis, 1993), but are valid only

under very limited conditions and during the growth period (Wilson, 1988).

Shank (1945) proposed that photosynthate partitioning is primarily determined by the ratio of carbon to nitrogen in plant organs. Based on this idea, Brouwer (1962) developed a model to simulate photosynthate partitioning and Thornley (1972) expressed Brouwer's model in the form of a series of mathematic equations. This kind of model has a clearer biological meaning and a strong mechanistic basis. However, due to difficulties in model parameterization, their application is very limited.

Several authors have developed a number of models of photosynthate partitioning in relation to source and sink (Thornley, 1976; Dewar, 1993; Minchin et al., 1993). Source–sink regulation models have been used with some success to simulate the assimilate partitioning (Coopers and Thornley, 1976; Minchin et al., 1994; Ho, 1996). The crucial step in this method is to determine the source and sink sizes, and create relevant equations to associate them. However, this method is only valid over limited phenological stages.

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Since Brouwer (1962, 1963) introduced the conception of functional equilibrium, this approach has been widely used to simulate photosynthate partitioning between shoot and root in plant vegetative growth (Brouwer and De Wit, 1969; De Willigen and Van Noordwijk, 1987). Based on the theory of functional equilibrium, many researchers used this approach to develop or extend their models to simulate assimilate partitioning for different crops and pastures (Davidson, 1969; Paltridge, 1970; Hunt and Burnett, 1973; Hunt and Nicholls, 1986; Van der Werf et al., 1993; Connor and Fereres, 1999).

Although many studies have been carried out on photosynthate partitioning, the models are poorly developed because assimilate partitioning involves many difficult problems in plant physiology (Ho, 1996) and its principle remains unclear (Enquist and Niklas, 2002). This paper presents a dynamic model that simulates the partitioning of crop biomass to leaf, stem and root, based on functional equilibrium, which resolves how crops adjust leaf transpiration and water uptake by the root in relation to water balance. The dynamic model has a good response to environmental factors, such as temperature, radiation, soil moisture and so on. The model was shown to perform well against experimental data of growth and partitioning of biomass in winter wheat over a 2-year period, when environmental factors varied and water supply was controlled over a wide range.

2. Model development

During the vegetative growth period, a wheat plant has three components, namely leaf, stem (and leaf sheath) and root. Assimilates are partitioned to the different components according to various partitioning coefficients. A diagram of the photosynthate partitioning model (PPModel) is shown in Fig. 1.

Through the accumulation of photosynthate formed in a day, the increments of plant leaf (ΔW_l), stem (ΔW_s) and root (ΔW_r) dry matter (DM) are:

$$\Delta W_l = mP_n \quad (1)$$

$$\Delta W_s = cmP_n \quad (2)$$

$$\Delta W_r = [1 - (1 + c)m]P_n \quad (3)$$

where m is the partition coefficient of assimilates to leaves, c the empirical parameter and P_n is the canopy net photosynthesis.

Gross photosynthesis is calculated according to the photosynthesis model proposed by Farquhar et al. (1980) and Van Caemmerer and Farquhar (1981):

$$P = \frac{\alpha I + P_{\max} - \sqrt{(\alpha I + P_{\max})^2 - 4\beta(\alpha I P_{\max})}}{2\beta} \quad (4)$$

where α is the initial photochemical efficiency, β the convexity, P_{\max} the photosynthetic rate at saturated light density, P the gross photosynthetic rate and I is the photosynthetic photon flux density. To consider the influence of water on photosynthesis, we proposed a linear correction factor, $f(\theta)$, for the above equation:

$$f(\theta) = \begin{cases} 0 & \theta \leq \theta_{wp} \\ (\theta - \theta_{wp})/(\theta_{ol} - \theta_{wp}) & \theta_{wp} \leq \theta \leq \theta_{ol} \\ 1 & \theta_{wp} \leq \theta \leq \theta_{ol} \\ 0.5 + 0.5(\theta - 1)/(\theta_{oh} - 1) & \theta_{ol} \leq \theta \leq \theta_{oh} \end{cases} \quad (5)$$

where θ is the volumetric soil water content and θ_{wp} the crop wilt point, and θ_{ol} and θ_{oh} the lower and upper limit of optimal water content. In Eq. (4), α is taken as a constant and P_{\max} is determined by the activity of Rubisco, in which the detailed calculation and the values for relevant parameters are referred to in the papers by Collatz et al. (1991) and Yu et al. (2002).

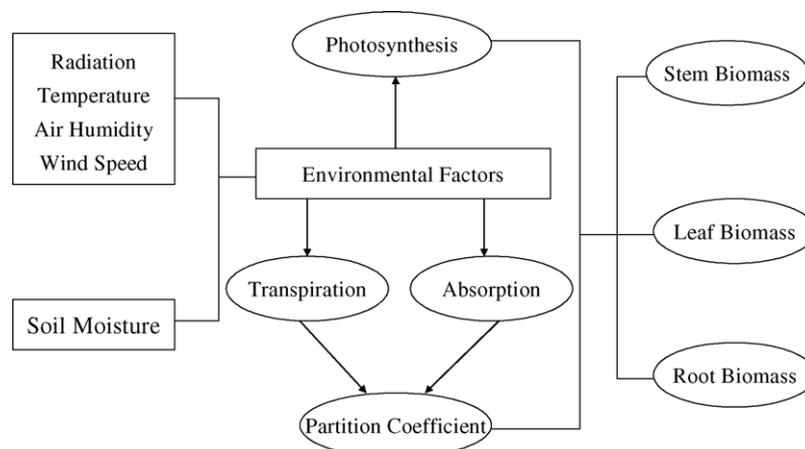


Fig. 1. Diagram of photosynthate partitioning model (PPModel).

Respiration consists of growth respiration (RG) and maintenance respiration (RM). Growth respiration is generally related to growth rate and maintenance respiration increases with plant size and temperature. The daily respiration rate can be calculated as follows (Penning de Vries et al., 1989):

$$R = \sum_1^3 RG_i + \sum_1^3 RM_i$$

$$= \sum_1^3 GE_i \frac{\Delta DM_i}{\Delta DM} + \sum_1^3 ME_i DM_i Q'_{10} (T_a - 25)^{10} \quad (6)$$

where GE is growth respiration coefficient, ME the maintenance respiration coefficient, ΔDM the increment of dry mass, Q'_{10} temperature coefficient for respiration and subscript i is equal to 1, 2, 3 and denotes leaf, stem and root, respectively.

Canopy net photosynthetic rate (P_n) is the integrations over the leaf layers and day length:

$$P_n = \int_0^{LAI} \int_{-\omega}^{\omega} P dL \cdot dw - R \quad (7)$$

where w is sunset hour angle and LAI is leaf area index.

The amount of water lost through transpiration (T_t) is determined by the leaf area and transpiration rate per unit leaf area (T_0). The specific leaf area (SLA) is assumed to be constant during the period of modeling, so T_t can be calculated as:

$$T_t = T_0 W_1 SLA = U W_1 \quad (8)$$

where T_0 is calculated by the S–W model (Shuttleworth and Wallace, 1985) and U is the transpiration per unit leaf dry weight.

Here, we adopt the classical root water-uptake model (Gardner, 1960; Herkelrath et al., 1977) with some minor revisions:

$$A_b = \frac{\theta}{\theta_s} E_r \frac{1}{WPL} (\psi_s - \psi_r) W_r = V W_r \quad (9)$$

where A_b is the amount of water absorbed by the root, θ the volumetric soil water contents, θ_s the field moisture capacity of the soil, E_r the root membrane permeability per unit length, ψ_s the average soil water potential at a depth of 120 cm, ψ_r the average water potential of plant root and WPL the dry weight of root per unit length, which can be obtained from the experimental data ($WPL = W_r/L$; L root length), and ψ_s is derived from the characteristic curve of soil water, using the Van Genuchten equation (Van Genuchten and Th., 1980) and V the rate of water absorbed per unit root dry weight.

Leaves are the major photosynthetic organ producing carbohydrate. The function of stems is to support the leaves and keep them well spread. The equilibrium between leaf and stem is assumed as a linear relation:

$$W_s = c W_1 + d \quad (10)$$

where c and d are empirical parameters fitted from experimental data.

Root growth is limited by the rate of supply of carbon from the leaves, whereas the growth of leaves is limited by the supply of water or nutrients from the root. The relationship between water consumption through transpiration and the water supply through root absorption from the soil should be satisfied with the following equation (Eq. (11)), and it can be assumed that the plant is in a functional equilibrium status (Shi and Wang, 1994):

$$T_t = K A_b \quad (11)$$

where K is a parameter, usually smaller than 1 because some of the water absorbed by the roots is lost through cutin transpiration used in growth.

If the plant is in a state of functional equilibrium, with dry weights of plant components W_1 , W_s and W_r , then Eqs. (10) and (11) will hold on each day:

$$W_s + \Delta W_s = c(W_1 + \Delta W_1) + d \quad (12)$$

$$U(W_1 + \Delta W_1) = KV(W_r + \Delta W_r) \quad (13)$$

Combining Eqs. (11)–(13), we get:

$$\Delta W_s = c \Delta W_1 \quad (14)$$

$$\Delta W_r = \frac{U}{KV} \Delta W_1 \quad (15)$$

Combining Eqs. (14) and (15), we get:

$$m P_n + c m P_n + \frac{U}{KV} m P_n = P_n \quad (16)$$

$$m \left(1 + c + \frac{U}{KV} \right) = 1 \quad (17)$$

then the partitioning coefficient m :

$$m = \frac{KV}{U + (1 + c)KV} \quad (18)$$

3. Materials and methods

3.1. Luancheng experiments

The experiments on winter wheat were conducted in 2002 and 2003 at Luancheng Comprehensive Experimental Station of Chinese Academy of Sciences, located in the North China Plain (NCP), 37°50'N, 114°40'E. There were 15 plots (5 m × 10 m) divided by concrete walls into five treatments. Each treatment represents one type of soil water-supply schedule (soil water content varied from 50 to 80% of field capacity, FC). Winter wheat, Gaoyou No. 503, was sown by hand at the rate of 150 kg ha⁻¹, in rows 20 cm wide. Crop measurements were taken weekly after wheat dormancy. The winter wheat plant is divided into leaf, stem (including sheath) and root. Ten randomly selected plants were harvested at

every sampling and oven-dried for 8–10 h. The dry matter of leaf and stem were weighed separately.

During the first 10 days of April in every experimental season, five soil samples (including wheat roots) were taken once from one plot of the five treatments with a special ‘root drill’ (similar to an auger), with a diameter of 5 cm and depth of 10 cm. The soil samples were soaked overnight in water to disperse the bulky clay soil. The roots were washed of soil onto a 1-mm sieve. Living roots were separated by hand from dead roots and debris. The root length was measured with a root-length scanner (Comair Root Length Scanner, Australia). The dry matter of roots was weighed after roots were oven-dried.

The purpose of the Luancheng experiments was to obtain the values of parameters c , d and WPL.

3.2. Yucheng experiments

The experiments were conducted in 2000 and 2001 at Yucheng Comprehensive Experimental Station of the Chinese Academy of Sciences, located in the NCP at 36°57'N, 116°36'E. Winter wheat plants, Gaoyou No. 503, were grown in six specially made steel buckets (1 × 1 × 1.77, length × width × depth), under a rainproof shelter. There were three treatments in which soil water content was controlled at 50 ± 5, 65 ± 5 and 80 ± 5% of FC (if the soil water content was less than the lower set limit, water was added by hand). Each treatment was replicated twice. At the bottom of the bucket, a layer of sand 27 cm in depth was added for draining through an access tube in the bucket base if soil water is too great. The buckets were filled with silt loam and optimal fertilizer. Soil water content and crop were measured after wheat dormancy. Daily values of soil water content and crop biomass were obtained from the measured data by linear interpolation.

Volumetric soil moisture was measured with a neutron probe (Institute of Hydrology, UK). Soil moisture and crop biomass were measured every 3 or 5 days. The plant was divided into leaf, stem (including sheath) and root after 10 single plants were harvested from the bucket and oven-dried for 8–10 h. The dry matter of leaf and stem were weighed. Meteorological data were taken from the station adjacent to the experimental station.

3.3. Statistic analysis

Root mean square error (RMSE) was used in this paper to estimate the differences between simulated and observed values:

$$\text{RMSE} = \sqrt{\frac{1}{M} \sum_{j=1}^M (Y_j - X_j)^2} \quad (19)$$

where M is the number of data points, Y_j and X_j are, respectively, the simulated and the observed values.

4. Model parameterization

All the values for the model parameters were determined from the literature, except for parameters c , d and WPL, which were calibrated from data from the Luancheng experiments.

The values of parameters c and d can be determined by fitting Eq. (11) to data on stem and leaf dry matter ($c = 1.21$, $d = -40 \text{ g m}^{-2}$). The value of parameter WPL can be determined according to the formula $\text{WPL} = \text{root dry matter} / \text{root length}$ ($\text{WPL} = 0.018 \text{ g m}^{-1}$).

5. Results

The independent data from the Yucheng experiments were used to test the PPMoDel. Using leaf and stem DM data from the Yucheng experiments, the empirical relationship between stem and leaf biomass can be verified. Fig. 2 shows a close linear relationship between stem and leaf biomass. Therefore, we can use the simple linear equation (Eq. (10)) to predict the growth relationship between leaf and stem, during the modeling period.

Both water consumption (calculated by S – W model) and water uptake (calculated by the ‘single root’ model) are potential values, and the comparison between them can demonstrate the validity of constructing the PPMoDel. The PPMoDel assumes the plant to be in functional equilibrium between water loss through leaf transpiration (T_t) and water uptake by the root (A_b). If the balance between them is disturbed, the plant adjusts itself through a change in the partitioning pattern to reach a new equilibrium in each day. Fig. 3 showed that the simulated T_t and KA_b have a close linear relationship, in accordance with the precondition of the PPMoDel, $T_t = KA_b$.

The comparison between the simulated and measured evapotranspiration was used to test the validity of the transpiration sub-model used in this paper and, thereby, justify the rationality of the core part of the PPMoDel. Fig. 4 shows that the simulated values agree approximately with the values measured by lysimeter, both in 2000 and in 2001.

Fig. 5 shows that the partitioning coefficient varies with U and V . The partitioning coefficient m increases with V . When the volumetric water content of soil increases, V will increase and more water will be absorbed by roots. Regulated by the functional equilibrium, photosynthates distributed to the leaves and the amount of water lost through leaf transpiration will increase (Garwood, 1968; Swanson et al., 1976) to reach a balance between water supply and consumption. This can well explain the following phenomena: (1) plants growing in semi-arid areas have opulent root systems. For example, in the Loess Plateau of China, the average depth of winter wheat roots is 3.7 m and the deepest can reach 5 m (Miao et al., 1989). However, in humid regions of South China, where precipitation is much higher than on the Loess Plateau, the average depth reached by

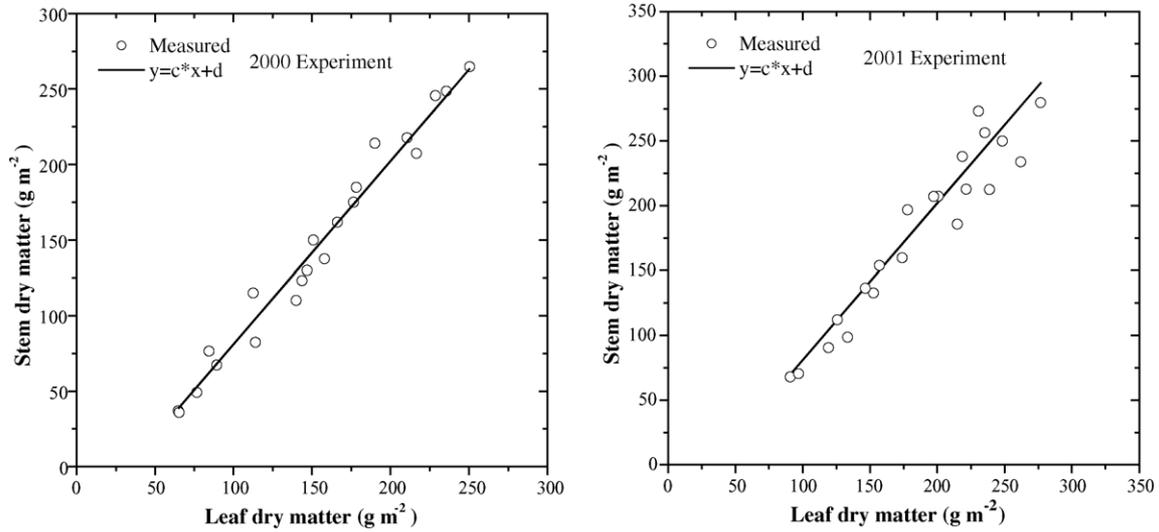


Fig. 2. Relationship between stem and leaf biomass.

winter wheat roots is only 1.6–1.8 m. (2) Plants process flourishing leaf clusters in abundant soil water conditions. If soil water is insufficient, root systems will flourish but leaves (aboveground organs) will grow thin. The partitioning coefficient m decreases with U . Air humidity has a direct influence on U . When air humidity increases, U will decrease and the partitioning coefficient m will increase. An increase in light intensity leads to an increase in stomatal conductance and acceleration of leaf photosynthesis. In terms of Eq. (18), U will increase, leading to a decrease in partitioning coefficient m , which agrees well with the result of Brouwer and De Wit (1969). Air temperature also significantly influences partitioning. On the one hand, an increase in temperature will increase the VPD and thus U . On the other hand, an increase in temperature also increases root membrane permeability and accelerates root absorp-

tion. Therefore, it is difficult to draw any conclusion about the effects of temperature on photosynthate partitioning; more research is needed on this issue (Coopers and Thornley, 1976).

Variations of the partitioning coefficient m are calculated by Eq. (18), under different environmental conditions in 2000 and 2001. Fig. 6 shows that the partitioning coefficient m at high soil water content is higher than that at lower water content. At high soil water content, roots have sufficient water for uptake and the plant will allocate more photosynthate to the above-ground organs (leaf and stem). The plant will also increase leaf area by a larger proportion to ‘consume’ the water, which can be absorbed by the roots from soil, thus reaching a new balance. At lower soil water content, less soil water can be absorbed by the root. Therefore, the plant will favor root growth, increase root

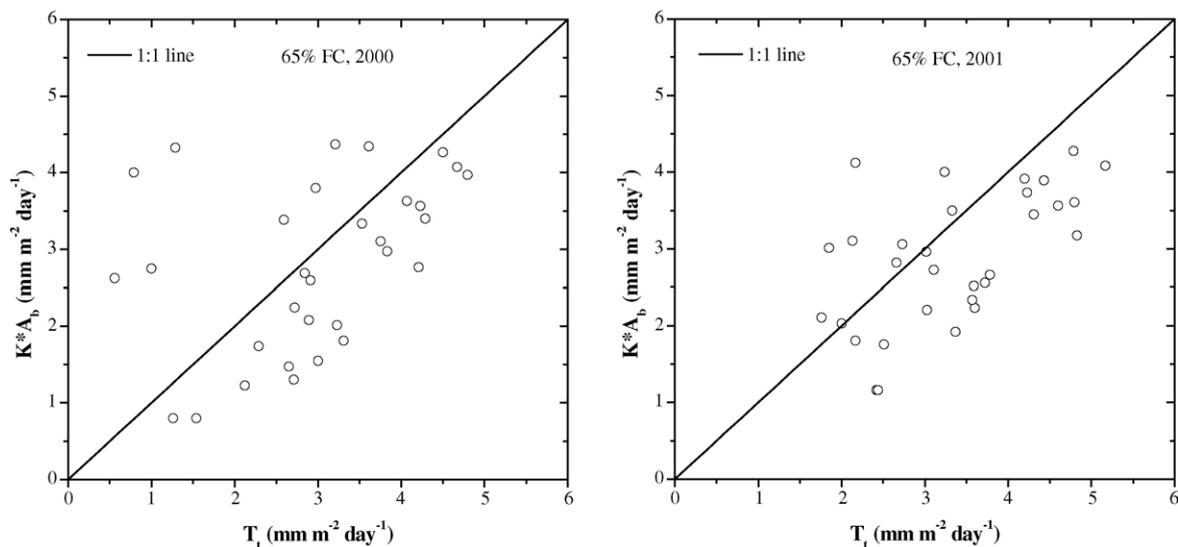


Fig. 3. Simulated T_r and A_b values.

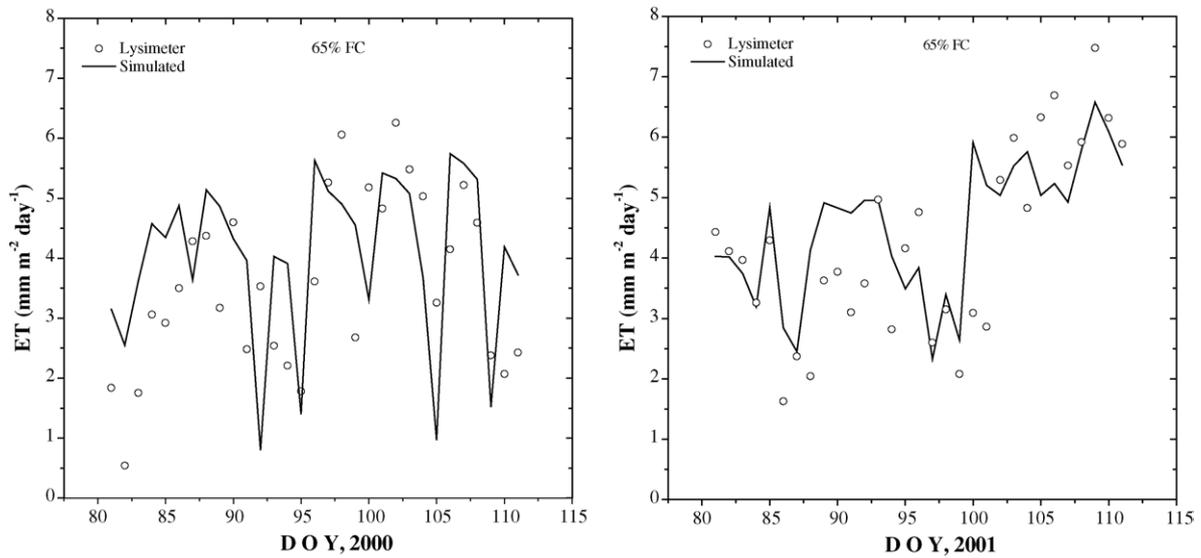


Fig. 4. Simulated ET and that measured by lysimeter.

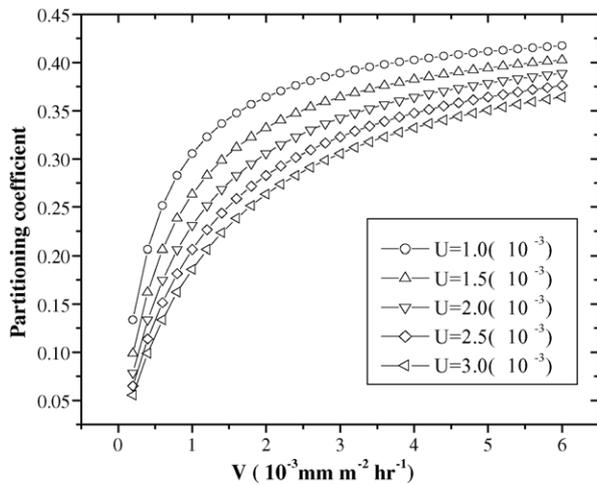


Fig. 5. Effects of environmental factors on partitioning coefficient *m*.

biomass to uptake more water and satisfy the need of leaf transpiration, so that it too reaches a balance.

The simulated curves and measured values of DM in leaf and stem (and sheath), under various soil conditions, are shown in Fig. 7. The simulated patterns for cumulative DM compares well with the measured values. At the beginning of the modeling period, leaf DM is greater than stem DM, but after Julian date 100 or so the stem DM exceeds leaf DM after wheat elongation. The intersection points between simulated leaf DM and stem DM curves demonstrate that the simulation agreed well with the real dynamic processes of winter wheat.

It is obvious that, in soil with adequate water content, the gross aboveground cumulative DM is higher than that in soil with lower water content. This shows good agreement with previous findings by Garwood (1968) and Swanson et al.

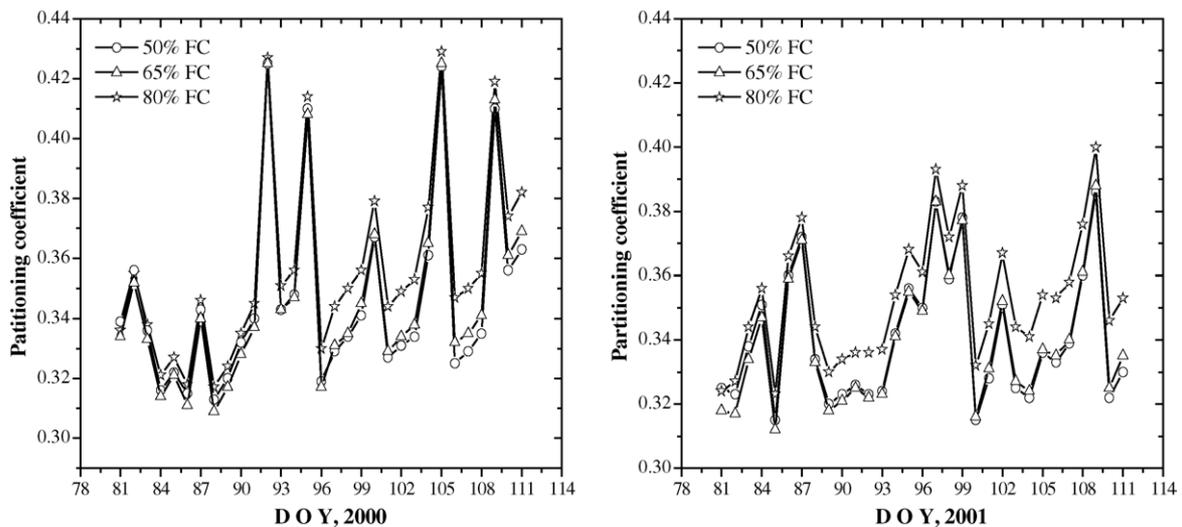


Fig. 6. Variation in partitioning coefficient *m*.

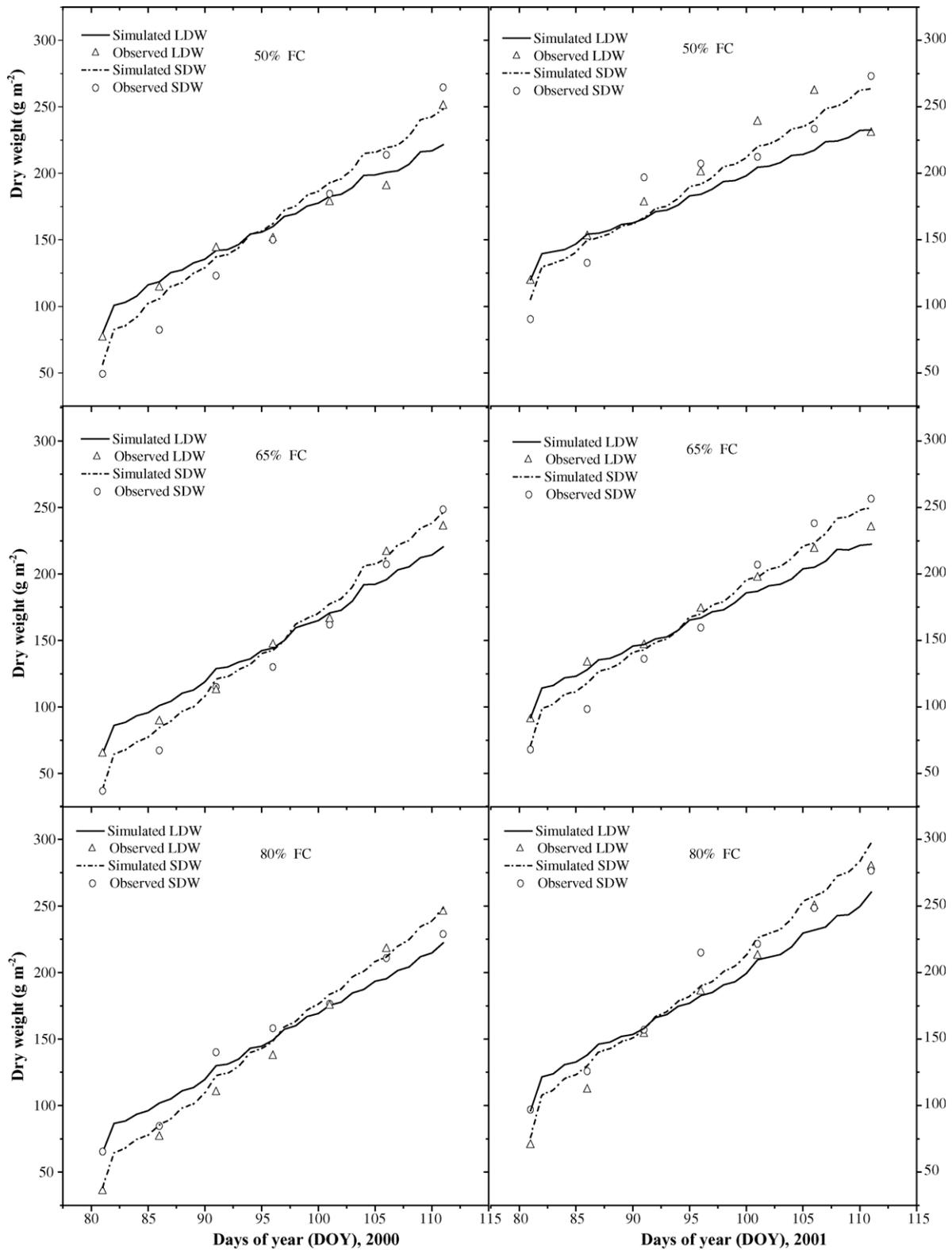


Fig. 7. Stem and leaf biomass accumulations.

(1976) that plants allocated more photosynthate to above-ground parts when there is abundant water in the soil.

The values of leaf and stem DM, obtained by RMSE, are shown in Table 1. RMSE values under various water

treatments are smaller than 25, showing that the PPMoDel can effectively simulate crop organ dry matter accumulation, when environmental factors varied daily and water supply was controlled over a wide range.

Table 1
Statistical analysis of the DM simulations (RMSE, gm^{-2})

Treatment (% FC)	2000		2001	
	Leaf DM	Stem DM	Leaf DM	Stem DM
50	12.56	13.64	22.66	16.35
65	10.55	10.65	8.87	11.25
80	10.38	8.38	11.58	16.31

6. Discussion and conclusion

The balanced state is easily disturbed by environmental changes. If the plant adjusts itself by a change in partitioning patterns, which can still return to the balance each day, the PPMoel will be valid. Otherwise, it will not be valid. Therefore, it is necessary to discuss partitioning when the plant cannot return to a balanced state on any day.

If the plant is in functional equilibrium at time t_1 , we have:

$$W_s = cW_1 + d \quad (20)$$

$$U_1 W_1 = KV_1 W_r \quad (21)$$

To ensure the plant will maintain its functional equilibrium state at time t_2 , the following relationships must hold:

$$W_s + \Delta W_s = c(W_1 + \Delta W_1) + d \quad (22)$$

$$U_2(W_1 + \Delta W_1) = KV_2(W_r + \Delta W_r) \quad (23)$$

Combining the above four equations, we can get the partitioning coefficient m , when a plant cannot return to its balanced state in 1 day:

$$m = \frac{KV_2}{U_2 + (1+c)KV_2} \left(1 - \frac{U_2/(KV_2)W_1 - W_r}{P_n} \right) \quad (24)$$

It is obvious that the value of m must be in the interval $[0, 1/(1+c)]$, because any DM formed once will be irremovable. If the value of m exceeds $1/(1+c)$, all assimilates will be allocated to the shoot. If the value of m is less than 0, all assimilates will be allocated to the root. Under these two conditions, the plant cannot maintain its functional equilibrium relationship in time interval t_1 to t_2 , and the model will not be valid.

This paper presents a dynamic photosynthate partitioning model that simulates the partitioning of crop biomass to leaf, stem and root, through the interaction between carbon gain (assimilation less respiration) and transpiration, both in relation to environmental factors. The environmental factors influence partitioning by affecting leaf transpiration and water absorption by root. Under conditions of high relative air humidity, sufficient soil water content and high light radiation, the plant will favor the growth of aboveground organs. Otherwise, the roots will have a higher priority to obtain photosynthate.

The PPMoel is based on the functional equilibrium theory and has the unique advantage in responding to

environmental factors, helping to perfect the crop growth model. However, its main disadvantage is that it is only applicable for the crop vegetative growing period.

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References

- Brouwer, R., 1962. Nutritive influences on distribution of dry matter in the plant. *Neth. J. Sci.* 10, 399–408.
- Brouwer, R., 1963. Some Aspects of the Equilibrium Between Overground and Underground Plant Parts. *Jaarboek Instituut voor Biologisch en Scheikundig onderzoek (IBS)*, pp. 31–39.
- Brouwer, R., De Wit, C.T., 1969. A simulation model of plant growth with special attention to root growth and its consequences. In: Whittington, W.J. (Ed.), *Root Growth*. Butterworth, London, pp. 224–244.
- Collatz, G.J., Ball, J.T., Grivet, C., Berry, J.A., 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agric. For. Meteorol.* 54, 107–136.
- Connor, D.J., Fereres, E., 1999. A dynamic model of crop growth and partitioning of biomass. *Field Crops Res.* 63, 139–157.
- Coopers, A.J., Thornley, J.H.M., 1976. Response of dry matter partitioning, growth, and carbon and nitrogen levels in the tomato plant to changes in root temperature: experiment and theory. *Ann. Bot.* 40, 1139–1152.
- Davidson, R.L., 1969. Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover. *Ann. Bot.* 33, 561–569.
- De Willigen, P., Van Noordwijk, M., 1987. *Roots, Plant Production and Nutrient Use*. Dissertation. Wageningen Agricultural University, Wageningen, 282 pp.
- Dewar, R.C., 1993. A root–shoot partitioning model based on carbon–nitrogen–water interactions and Munch phloem flow. *Funct. Ecol.* 7, 356–368.
- Enquist, B.J., Niklas, K.J., 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295, 1517–1520.
- Farquhar, G.D., von Caemmerer, S., Berry, J.A., 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 plants. *Planta* 149, 78–90.
- Gardner, W.R., 1960. Dynamic aspects of water availability to plants. *Soil Sci.* 89, 63–73.
- Garwood, E.A., 1968. Some effects of soil water conditions and temperature on the roots of grasses and clovers. II. Effects of variation in the soil water content and in soil temperature on root growth. *J. Br. Grassl. Soc.* 23, 117–128.
- Herkelrath, W.N., Miller, E.E., Gardner, W.R., 1977. Water uptake by plants. II. The root contact model. *Soil Sci. Am. J.* 41, 1039–1043.
- Ho, L.C., 1996. Tomato. In: Zemaski, E., Schaffer, A.A. (Eds.), *Photoassimilate Distribution in Plants and Crops: Source–Sink Relationships*. Marcel Dekker, New York, pp. 709–728.
- Hoogenboom, G., Jones, J.W., Boote, K.J., 1992. Modelling growth, development and yield of grain legumes using SOYGRO, PNUTGRO and BEANGRO: a review. *Trans. Am. Soc. Agric. Eng.* 35, 2043–2056.

- Hunt, R., Nicholls, A.O., 1986. Stress and the course control of growth and root–shoot partitioning in herbaceous plants. *Oikos* 47, 149–158.
- Hunt, R., Burnett, J.A., 1973. The effects of light intensity and external potassium level on root/shoot ratio and rates of potassium uptake in perennial ryegrass (*Loium perenne* L.). *Ann. Bot.* 39, 519–537.
- Marcelis, L.F.M., 1993. Simulation of biomass allocation in greenhouse crops: a review. *Acta Hort.* 328, 49–67.
- Miao, G.Y., Zhang, Y.T., Yin, J., Hou, Y.S., Pan, X.L., 1989. A study on the development of root system in winter wheat under unirrigated conditions in semi-arid Loess Plateau. *Acta Agron. Sinc.* 15, 104–115 (in Chinese).
- Minchin, P.E.H., Thorpe, M.R., Farrar, J.F., 1993. A simple mechanistic model of phloem transport which explains sink priority. *J. Exp. Bot.* 44, 947–955.
- Minchin, P.E.H., Thorpe, M.R., Farrar, J.F., 1994. Short term control of root:shoot partitioning. *J. Exp. Bot.* 45, 615–622.
- Paltridge, G.W., 1970. A model of a growing pasture. *Agric. Meteorol.* 7, 93–130.
- Penning de Vries, F.W.T., Jansen, D.M., ten Berge, H.F.M., Bakema, A., 1989. Simulation of Ecophysiological Processes of Growth in Several Annual Crops. Pudoc, Wageningen, pp. 82–96.
- Penning de Vries, F.W.T., van Laar, H.H., 1982. Simulation of Plant Growth and Crop Production. Pudoc, Wageningen, pp. 27–42.
- Shank, D.B., 1945. Effects of phosphorus, nitrogen, and soil moisture on top–root ratios of inbred and hybrid maize. *J. Agric. Res.* 70, 365–377.
- Shi, J.Z., Wang, T.D., 1994. A mechanistic model describing the photosynthate partitioning during vegetative phase. *Acta Bot. Sin.* 36, 181–189 in Chinese.
- Shuttleworth, W.J., Wallace, J.S., 1985. Evaporation from sparse crops: an energy combination theory. *Quart. J. R. Meteorol. Soc.* 111, 839–855.
- Supit, I., Hooijer, A.A., Van Diepen, C.A., 1994. System Description of the WOFOST 6.0 Crop Simulation Model Implemented in CGMS.
- Swanson, C.A.J., Hoddinott, J., Sij, J.W., 1976. The selected sink leaf parameters on translocation rates. In: Wardlaw, I.F., Passioure, J.B. (Eds.), *Transport and Transfer Process in Plants*. Academic Press, New York, pp. 347–356.
- Thornley, J.H.M., 1972. A balanced quantitative model for root/shoot ratios in vegetative plants. *Ann. Bot.* 36, 431–441.
- Thornley, J.H.M., 1976. *Mathematical Models in Plant Physiology*. Academic Press, London, 318 pp.
- Van Caemmerer, S., Farquhar, G.D., 1981. Some relationship between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153, 376–387.
- Van der Werf, A., Enserink, T., Smit, B., Booi, R., 1993. Allocation of carbon and nitrogen as a function of the internal nitrogen status of a plant: modelling allocation under non-steady-state situations. *Plant Soil* 155/156, 183–186.
- Van Genuchten, M.Th., 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Sci. Soc. Am. J.* 44, 892–898.
- Wardlaw, I.F., 1990. The control of carbon partitioning in plants. *New Phytol.* 116, 341–381.
- Williams, J.R., Jones, C.A., Kiniry, J.R., Spanel, D.A., 1989. The EPIC crop growth model. *Trans. Am. Soc. Agric. Eng.* 32, 497–511.
- Wilson, J.B., 1988. A review of evidence on the control of shoot:root ratio, in relation to models. *Ann. Bot.* 61, 433–449.
- Yu, Qiang, Liu, Yenfen, Liu, Jiandon, Wang, Tianduo, 2002. Simulation of leaf photosynthesis of winter wheat on Tibetan plateau and in north China plain. *Ecol. Model.* 155, 205–216.