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Integrating Photosynthesis, Respiration, Biomass Partitioning, and Plant Growth: Developing a Microsoft Excel®-based Simulation Model of Wisconsin Fast Plant (*Brassica rapa*, Brassicaceae) Growth with Undergraduate Students

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Abstract. This paper demonstrates the development of a simple model of carbon flow during plant growth. The model was developed by six undergraduate students and their instructor as a project in a plant ecophysiology course. The paper describes the structure of the model including the equations that were used to implement it in Excel®, the plant growth experiments that were conducted to obtain information for parameterizing and testing the model, model performance, student responses to the modeling project, and potential uses of the model by other students.

Key words: carbon flow, partitioning, photosynthesis, plant growth, potential relative growth rate, respiration, simulation model, student learning, Wisconsin Fast Plants
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1. Introduction to modeling plant growth

As plants grow, they add and enlarge leaves, stems, roots, flowers, and fruits, organs which are composed of water and carbon-based dry matter in the form of carbohydrates, lipids, proteins, and other molecules. People who are interested in following or predicting plant growth generally focus on carbon flow in the form of dry mass rather than total plant mass because plant water content depends on the quantity of dry matter present, the type of plant and plant part, and environmental conditions. Examining the acquisition and flow of dry mass within plants requires integration of information about photosynthesis, the process that brings the vast majority of dry mass into a plant; respiration, the process that releases stored chemical energy from dry mass when it is needed to run plant processes; and the partitioning of recently acquired dry mass to different plant organs [5]. Unfortunately, students at all levels have misconceptions about these processes [7, 8, 16], and have difficulty tracing the flow of matter through biological systems [39]. A variety of simulation models have been developed to explore the interaction among processes involved in plant growth (reviewed in [23, 26, 34, 36]), but professional models of plant growth are not accessible to students who are just beginning to explore the topic. In this paper, we demonstrate the development of a simple simulation model of the leaf, stem, and root growth of Wisconsin Fast Plants (rapid cycling *Brassica rapa*) by six undergraduate students and their instructor. Other students may use the information in this paper to repeat the process of model development and/or use the completed model to explore plant growth.

We chose to model the carbon flow in Wisconsin Fast Plants because these plants have been selected to grow rapidly under continuous illumination and are frequently used in classroom learning [11, 38]. They complete their life cycle within approximately 45 days, first producing leaves, stems, and roots, collectively called vegetative plant parts, and then producing flowers and fruits [11]. We restricted the model to vegetative growth to keep the model simple. The Wisconsin Fast Plant Growth Model was developed as a highly simplified version of PEACH, a simulation model of the vegetative and reproductive growth of a peach (*Prunus persica*) tree [14, 15]. We chose to implement the Wisconsin Fast Plant Growth Model in Microsoft Excel® (Microsoft Corporation, Redmond, Washington, USA) because this program is widely available and familiar to many students.

2. Context for the development of the plant growth model

Five senior biology undergraduates (ABB, MLC, LRF, SFP, KSS) who were enrolled in a one-semester advanced biology course in plant ecophysiology chose to participate in the model construction project with their instructor (YLG). Two of the students had taken an introductory botany course and all of the students had taken an experimental design and statistics course. In addition to the modeling project, the seminar-style course addressed physiological and environmental aspects of photosynthesis and respiration at the individual plant and ecosystem levels. In the laboratory portion of the course, groups of students conducted initial experiments to learn laboratory techniques and then completed the plant growth studies described in the next section. To learn about simulation modeling, the students engaged in activities that used two simulation modeling pro-

grams, PEACH [14, 15], and Environmental Decision Making (EDM; [30]), a model of the flow of energy and carbon in simulated pond, grassland, and forest ecosystems. After the end of the course, one student (AJS) who had not taken the plant ecophysiology course continued the modeling project during an eight-week summer research program and obtained the data used for the final version of the model.

3. Development of the Wisconsin Fast Plant Growth Model

3.1. Model structure

The Wisconsin Fast Plant Growth Model simulates the flow of carbon during plant growth using the economic concepts of supply and demand to describe plant growth ([5], Figure 1) . Photosynthesis provides the supply of carbon in the form of carbohydrate by capturing or "fixing" carbon dioxide from the atmosphere using light energy. The demand for carbon comes from maintenance respiration and growth. Maintenance respiration involves the release of stored chemical energy and carbon dioxide from carbohydrate. Because the energy that is released is used to conduct chemical reactions necessary for the plant's existence, maintenance respiration may be called "the cost of staying alive." Growth is the increase in dry mass of plant organs and may involve the production of new organs and/or the enlargement of existing organs. The chemical reactions that occur during growth convert carbohydrate to other forms of plant dry mass, a process that requires energy, which is made available through growth respiration, releasing carbon dioxide. As in other economic systems, demand may exceed supply but plants cannot borrow from a "bank" outside their own structures, so the supply of dry matter limits their demand activity.

The model represents hypotheses about carbon flow and the accumulation of structural and storage biomass resulting from photosynthesis, respiration, and the partitioning of carbohydrate to different plant parts [5, 10, 38]. In the modeling context, these quantities are called "state variables" because they represent the state or condition of the system [10, 17, 35]. The processes that relate the state variables to one another are characterized by equations; the coefficients in these equations are referred to as "parameters" [35]. The state variables and parameters of the model are listed in Tables 1 and 2.

3.2. Carbon supply

Photosynthesis provides the supply of dry matter in the form of carbohydrate by acquiring carbon dioxide from the atmosphere using light energy (Figure 1). In the model, we assumed that all leaves are equally illuminated (i.e., no self-shading occurs) and photosynthesize at the same rate. The model simulates the quantity of carbohydrate produced by photosynthesis ($CHO_{GrossPs}$, Table 1) as the product of the gross photosynthetic rate (GrossPsRate), leaf area ($Area_{Leaf}$), and light period (LightPeriod).

$$CHO_{GrossPs} = GrossPsRate * Area_{Leaf} * LightPeriod \tag{3.1}$$

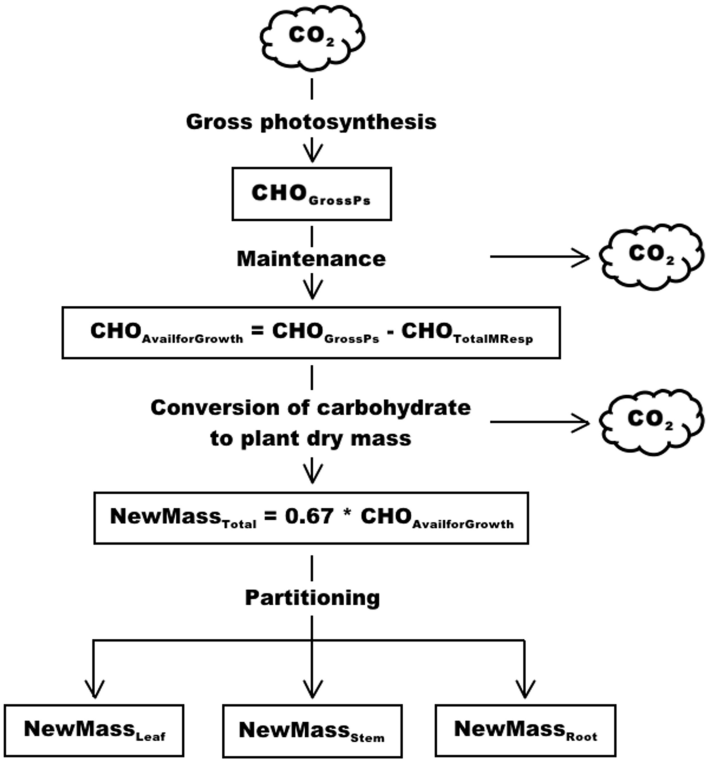


Figure 1: Simplified model of the flow of carbon within a plant in one day. Clouds and boxes represent carbon pools and arrows represent processes that convert carbon-containing molecules from one form to another. The plant acquires carbon from carbon dioxide through photosynthesis. Some of the newly acquired carbon is used in maintenance respiration and released from the plant as carbon dioxide. The remaining carbon is converted to plant dry mass in a process that requires energy from carbohydrate and releases carbon dioxide. The plant dry mass is divided ("partitioned") to leaves, stems, and roots. Adapted from [10, 14].

The gross photosynthetic rate is the sum of the net photosynthetic rate (NetPsRate) and the leaf maintenance respiration rate ($MResp_{Leaf}$) during illumination, which is generally assumed to equal the dark respiration rate [2]. The gross photosynthetic rate cannot be measured directly because doing so would require elimination of maintenance respiration and, hence, the death of the leaf. Thus, laboratory and field studies of photosynthesis generally report net rather than gross photosynthetic rates.

3.3. Carbon demand for maintenance respiration

Maintenance respiration is required for living cells to remain alive. The carbohydrate need for maintenance respiration for each type of organ (CHO_{XMResp}) is simulated as the product of the maintenance respiration rate ($MRespRate_X$), the dry mass of organ ($Mass_X$), and the number of

Table 1: The state variables, symbols, units, equation numbers, and location in the Excel spreadsheet for the Wisconsin Fast Plant Growth Model. State variables are updated each day, but the time subscripts are not shown for simplicity. Abbreviations: CHO=carbohydrate, d=day, DM=dry matter, g=gram, m=meter.

State variable	Symbol	Units	Equation number in text	Location in Excel spreadsheet
Carbohydrate quantities				
Gross photosynthesis	$CHO_{GrossPs}$	μg CHO plant^{-1} d^{-1}	3.1	F19–F29
Leaf maintenance respiration	$CHO_{LeafMResp}$	μg CHO plant^{-1} d^{-1}	3.2	G19–G29
Stem maintenance respiration	$CHO_{StemMResp}$	μg CHO plant^{-1} d^{-1}	3.3	H19–H29
Root maintenance respiration	$CHO_{RootMResp}$	μg CHO plant^{-1} d^{-1}	3.4	I19–I29
Total maintenance respiration	$CHO_{TotalMResp}$	μg CHO plant^{-1} d^{-1}	3.5	J19–J29
Carbohydrate available for growth	$CHO_{AvailforGrowth}$	μg CHO plant^{-1} d^{-1}	3.10	K19–K29
Growth demand				
Leaf potential demand	$PotDemand_{Leaf}$	g DM plant^{-1} d^{-1}	3.6	M19–M29
Stem potential demand	$PotDemand_{Stem}$	g DM plant^{-1} d^{-1}	3.7	N19–N29
Root potential demand	$PotDemand_{Root}$	g DM plant^{-1} d^{-1}	3.8	O19–O29
Total potential demand	$PotDemand_{Total}$	g DM plant^{-1} d^{-1}	3.9	P19–P29
Ratio of dry matter available to total demand	SupplyDemandRatio	–	3.12	Q19–Q29
Proportion of growth allowed	PropAllowed	–	3.13/3.14	R19–R29
Day	Day	d	3.19	A19–A29
Plant characteristics				
Leaf dry mass	$Mass_{Leaf}$	g DM plant^{-1}	3.20	B19–B29
Stem dry mass	$Mass_{Stem}$	g DM plant^{-1}	3.21	C19–C29
Root dry mass	$Mass_{Root}$	g DM plant^{-1}	3.22	D19–D29
Leaf mass added	$NewMass_{Leaf}$	g DM plant^{-1}	3.15	S19–S29
Stem mass added	$NewMass_{Stem}$	g DM plant^{-1}	3.16	T19–T29
Root mass added	$NewMass_{Root}$	g DM plant^{-1}	3.17/3.18	U19–U29
Total dry mass added	$NewMass_{Total}$	g DM plant^{-1}	3.11	L19–L29
Leaf area	$Area_{Leaf}$	m^2	3.23	E19–E29

seconds in a day, 86400, because plant organs respire continuously.

$$CHO_{LeafMResp} = MRespRate_{Leaf} * Mass_{Leaf} * 86400 \tag{3.2}$$

$$CHO_{StemMResp} = MRespRate_{Stem} * Mass_{Stem} * 86400 \tag{3.3}$$

$$CHO_{RootMResp} = MRespRate_{Root} * Mass_{Root} * 86400 \tag{3.4}$$

The total maintenance respiration ($CHO_{TotalMResp}$) is the sum of the leaf, stem, and root maintenance respiration.

$$CHO_{TotalMResp} = CHO_{LeafMResp} + CHO_{StemMResp} + CHO_{RootMResp} \tag{3.5}$$

Table 2: Parameters, symbols, default values, units, and location in the Excel spreadsheet for the Wisconsin Fast Plant Growth Model. Abbreviations: CO_2=carbon dioxide, d=day, DM=dry matter, g=gram, h=hour, m=meter, mol=mole, s=second.

Parameter	Symbol	Default value	Units	Location in Excel spreadsheet
Light period	LightPeriod	24	h	C4
Photosynthetic parameters				
Net photosynthetic rate	NetPsRate	8.5	μmol CO_2 m^{-2} s^{-1}	C5
Gross photosynthetic rate	GrossPsRate	9.0	μmol CO_2 m^{-2} s^{-1}	C6
Maintenance respiration parameters				
Leaf maintenance respiration rate	$MRespRate_{Leaf}$	0.0250	μmol CO_2 g^{-1} s^{-1}	C7
Stem maintenance respiration rate	$MRespRate_{Stem}$	0.0125	μmol CO_2 g^{-1} s^{-1}	C8
Root maintenance respiration rate	$MRespRate_{Root}$	0.0125	μmol CO_2 g^{-1} s^{-1}	C9
Potential growth parameters				
Leaf potential RGR	PotRGRLeaf	0.398	g DM (g DM)$^{-1}$ d^{-1}	K6
Intercept for leaf RGR equation	–	-6.64	–	J6
Stem potential RGR	PotRGRStem	0.456	g DM (g DM)$^{-1}$ d^{-1}	K7
Intercept for stem RGR equation	–	-8.45	–	J7
Root demand	RootDemand	0.2	–	K8
Leaf mass to area ratio	LeafMass/Area	20	g DM m^{-2}	J12

3.4. Carbon demand for potential growth

Plants use the dry matter produced each day to grow, but the potential for growth often exceeds the supply of dry matter available on any given day. Partitioning is the term applied to the set of processes that determine how much of the available dry matter each organ receives (Figure 1). One partitioning hypothesis states that competition among organs determines the amount of dry matter that an organ receives, and that this competition is based upon each organ's "potential demand," the amount the organ is capable of growing on a given day [12, 13, 14, 25, 37]. For example, the maximum amount that the dry mass of a leaf can increase in one day is dictated by the number of cells present, the number added by cell division, and the maximum expansion rate for each cell [25]. Similarly, the amount of dry mass that a small, young pumpkin can incorporate on one day is much less than the amount that a nearly mature, large pumpkin can use. We may characterize the potential demand in terms using the potential relative growth rate (PotRGRX, g DM (g DM)$^{-1}$ d^{-1}), the maximum amount of dry mass that one gram of an organ can add in one day [12, 13, 14, 24, 25]. The potential RGR for each organ is analogous to its maximum possible interest rate. The potential demand ($PotDemand_X$) for dry matter by each organ type is simulated using exponential growth equations and the current dry mass of the organ ($Mass_X$; Appendix I).

$$PotDemand_{Leaf} = Mass_{Leaf} * (e^{PotRGRLeaf} - 1) \tag{3.6}$$

$$PotDemand_{Stem} = Mass_{Stem} * (e^{PotRGRStem} - 1) \tag{3.7}$$

Because little information is available about the growth potential of roots [23], the model simulates root potential demand ($\text{PotDemand}_{\text{Root}}$) as a proportion (RootDemand) of stem potential demand ($\text{PotDemand}_{\text{Stem}}$). Model users may manipulate this proportion.

$$\text{PotDemand}_{\text{Root}} = \text{RootDemand} * \text{PotDemand}_{\text{Stem}} \tag{3.8}$$

The total potential demand for plant dry matter ($\text{PotDemand}_{\text{Total}}$) is the sum of the leaf, stem, and root potential demand.

$$\text{PotDemand}_{\text{Total}} = \text{PotDemand}_{\text{Leaf}} + \text{PotDemand}_{\text{Stem}} + \text{PotDemand}_{\text{Root}} \tag{3.9}$$

3.5. Reconciliation of supply and demand

The model determines the amount of carbohydrate available for growth ($\text{CHO}_{\text{AvailforGrowth}}$) by subtracting the carbohydrate needed for the maintenance respiration of all plant parts from the carbohydrate produced by photosynthesis (Figure 1).

$$\text{CHO}_{\text{AvailforGrowth}} = \text{CHO}_{\text{GrossPs}} - \text{CHO}_{\text{TotalMResp}} \tag{3.10}$$

During growth, the carbohydrate available for growth is converted to many different types of molecules, which requires energy from carbohydrate for growth respiration and releases carbon dioxide [5, 10, 22, 28, 35]. This conversion occurs with an efficiency of approximately 67% [22], producing the dry matter added to the plant ($\text{NewMass}_{\text{Total}}$).

$$\text{NewMass}_{\text{Total}} = 0.67 * \text{CHO}_{\text{AvailforGrowth}} \tag{3.11}$$

Most of the time, the potential demand for organ growth ($\text{PotDemand}_{\text{Total}}$) exceeds the supply of available dry mass ($\text{NewMass}_{\text{Total}}$). Because the model uses the hypothesis that organs compete for dry matter based on their potential demand, the ratio of supply to demand determines the proportion of potential growth allowed (SupplyDemandRatio) for each organ [14, 24, 25].

$$\text{SupplyDemandRatio} = \text{NewMass}_{\text{Total}}/\text{PotDemand}_{\text{Total}} \tag{3.12}$$

If the supply of dry matter is less than the demand, then the proportion of demand allowed (Prop Allowed) is set to the supply-demand ratio, otherwise the proportion of demand allowed is set to 1.

$$\text{If SupplyDemandRatio} < 1, \text{PropAllowed = SupplyDemandRatio} \tag{3.13}$$

$$\text{If SupplyDemandRatio} \geq 1, \text{PropAllowed} = 1 \tag{3.14}$$

In either case, the new mass of leaves ($\text{NewMass}_{\text{Leaf}}$) and stems($\text{NewMass}_{\text{Stem}}$) is the product of the proportion of growth allowed and their demands.

$$\text{NewMass}_{\text{Leaf}} = \text{PropAllowed} * \text{PotDemand}_{\text{Leaf}} \tag{3.15}$$

$$\text{NewMass}_{\text{Stem}} = \text{PropAllowed} * \text{PotDemand}_{\text{Stem}} \tag{3.16}$$

If the supply of dry matter available for growth is equal to or less than the demand, the new mass of roots ($\text{NewMass}_{\text{Root}}$) is proportional to root demand.

$$\text{NewMass}_{\text{Root}} = \text{PotDemand}_{\text{Root}} * \text{PropAllowed} \tag{3.17}$$

If the supply of dry matter available for growth exceeds the potential demand, the dry matter in excess of the potential demand is added to the roots.

$$\text{NewMass}_{\text{Root}} = \text{PotDemand}_{\text{Root}} + (\text{NewMass}_{\text{Total}} - \text{PotDemand}_{\text{Total}}) \tag{3.18}$$

Each day, the model increments the day counter by 1 and the leaf, stem, and root dry mass is updated by adding the amount of new dry mass produced on the previous day to the previous day's value.

$$\text{Day}_{\text{T}} = \text{Day}_{\text{T - 1}} + 1 \tag{3.19}$$

$$\text{Mass}_{\text{Leaf,T}} = \text{NewMass}_{\text{Leaf, T -1}} + \text{Mass}_{\text{Leaf, T -1}} \tag{3.20}$$

$$\text{Mass}_{\text{Stem,T}} = \text{NewMass}_{\text{Stem, T -1}} + \text{Mass}_{\text{Stem, T -1}} \tag{3.21}$$

$$\text{Mass}_{\text{Root,T}} = \text{NewMass}_{\text{Root, T -1}} + \text{Mass}_{\text{Root, T -1}} \tag{3.22}$$

Leaf area ($\text{Area}_{\text{Leaf,T}}$) is calculated by dividing the leaf mass by the parameter for the ratio of leaf mass to area (LeafMass/Area).

$$(\text{Area}_{\text{Leaf,T}}) = \text{Mass}_{\text{Leaf,T}}/(\text{LeafMass/Area}) \tag{3.23}$$

3.6. Model implementation

The Wisconsin Fast Plant Growth Model was developed using Excel® software (Microsoft Corporation, Redmond, Washington, USA). Model parameters for growth were estimated using the measured plants as described in the next section (Table 2). Simulated and measured leaf and stem dry mass were compared by regressing the measured values on the simulated values and examining the slopes and intercepts of the regression lines to test our hypotheses about plant growth and partitioning [31]. The sensitivity of the model to changes in input values was examined by systematically changing model parameters by 10% [17].

4. Plant growth

4.1. Experimental methods

Wisconsin Fast Plants were grown from seed (Standard, improved basic, Rbr, # 158805, Carolina Biological Supply, Burlington, North Carolina, USA) in film can wickpots designed to supply water and nutrients to the plants [11]. Two seeds were planted in each wickpot after filling with Fafard Superfine Germinating Soil (Agawam, Massachusetts, USA) and two pellets of NPK (14-14-14) slow-release fertilizer pellets. Five wickpots were placed in a pint-sized delicatessen container

nested within a reservoir made from a quart-sized delicatessen container [11]. The floor of each pint container was covered by an 8 cm diameter "lollipop" of capillary mat. The "lollipop handle" (1.5 cm $\times$ 7 cm) was threaded through a slit in the bottom of the pint container and immersed in the liquid in the quart container, which consisted of approximately 200 ml distilled water adjusted to 0.01% copper sulfate to prevent algal growth [40]. Soil, fertilizer, and capillary mats were obtained from Carolina Biological Supply.

The plants were grown in boxes (46 cm high $\times$ 46 cm wide $\times$ 31 cm deep) that were lined with aluminum foil and had a foil curtain that covered the box opening [11]. Plants were illuminated with two helical compact fluorescent bulbs (26 watts each). The mean light intensity 6 cm below the bottom of the compact fluorescent bulbs was 282 μmol m^{-2} s^{-1} (SE = 9.0) and there was no effect of position within the box. Plants were grown under continuous illumination (24 h) or alternating periods of 14 h light and 10 h dark. Temperature in the growth boxes was approximately 23 °C.

Wickpots were thinned to one plant per pot after the cotyledons emerged from the soil. Beginning on the third day after planting, 10 plants per light treatment were harvested at two-day intervals, separated into leaves and stems, dried at 66 °C for 24–48 h, and weighed. The area of selected leaves was measured using a transparent grid prior to drying in order to determine the relationship between leaf area and leaf mass. Root dry mass was not measured because roots could not be separated from the growth medium.

Analysis of covariance (ANCOVA) was used to examine the effects of light period, organ type, and time since planting on leaf and stem mass. Prior to performing the ANCOVA, leaf and stem dry mass data from each treatment were logarithmically-transformed to normalize their distributions and equalize their variances. All statistical analyses were completed in JMP (Version 8.0, SAS Institute, Cary, North Carolina, USA).

4.2. Experimental results

Under the growth conditions, the cotyledons of plants grown under both light conditions emerged on day 1, the day after planting. Flower buds and open flowers were present on some plants on day 13. For this reason and because plants were harvested every other day beginning on day 3, we constructed a model of the first 11 days of vegetative growth.

The Wisconsin Fast Plants grew significantly over time (significant effect of time since planting), and they grew significantly more leaf and stem dry mass under 24 h illumination than 14 h illumination (significant effect of light period; Table 3). Stems accumulated dry mass faster than leaves (significant effect of interaction between organ type and time since planting), but had less mass than leaves because they started with substantially less mass than leaves (significant effect of organ type; Tables 3, 4; Figure 2). Exponential equations fit leaf and stem growth under both 24 and 14 h illumination as indicated by significant linear relationship between days after planting and logarithmically-transformed dry mass (Table 4; Figure 2). The exponential equations accounted for 86–94% of the observed variability, although deviations from linearity were detected, indicating that more complex equations would have accounted for even more of the observed variation.

Table 3: Results of the analysis of covariance of the effect of light period, organ type, and time since planting on logarithmically-transformed leaf and stem dry mass for Wisconsin Fast Plants grown under 24 and 14 h illumination.

Source	DF	Sum of Squares	F Ratio	P-value
Light period	1	19.6	131	< 0.0001
Organ type	1	99.6	667	< 0.0001
Time since planting	1	269	1803	< 0.0001
Light period x Organ Type	1	0.0313	0.210	0.65
Light period x Time since planting	1	0.247	1.65	0.20
Organ type x Time since planting	1	1.20	8.04	0.0051
Light period x Organ type x Time since planting	1	0.00296	0.0198	0.89
Error	190	28.4		

Table 4: Intercept, coefficient, proportion of variation explained by regression (R^2), F ratio, and probability value for linear regression of logarithmically-transformed leaf and stem dry mass on time since planting.

Light period	Organ type	Intercept	Coefficient	R^2	F Ratio	P-value
24 h	Leaves	-6.64	0.398	0.922	551	< 0.0001
24 h	Stems	-8.45	0.456	0.856	280	< 0.0001
14 h	Leaves	-7.09	0.376	0.942	783	< 0.0001
14 h	Stems	-8.90	0.429	0.921	558	< 0.0001

5. Model results

5.1. Parameterizing the model

The Wisconsin Fast Plants grew to the greatest extent under 24 h illumination, so we used the data from these plants to determine the potential RGRs for leaves and stems (PotRGRLeaf, PotRGRStem) from the slope of the regressions between the log-transformed dry masses and time (Table 4; Figures 2C,D). The potential RGRs for leaves and stems were 0.398 and 0.456 g DM (g DM)$^{-1}$d^{-1}, respectively. The initial leaf and stem dry mass on the first day after planting were 1.946 and 0.337 mg, respectively. Because root dry weight was not measured in the experiment, root potential RGR (PotRGRRoot) and the initial root mass ($\text{Mass}_{\text{Root}}$) were set to a proportion of the stem values (RootDemand). Leaf area was determined from leaf dry mass using a leaf dry mass to area ratio (LeafMass/Area). In the simulations presented here, RootDemand was set to 0.2 and LeafMass/Areas was set to 20 g DM m^{-2}. Model users may adjust both values.

The leaf maintenance respiration rate ($\text{MRespRate}_{\text{Leaf}}$) was set to 25 nmol CO_2 g^{-1} s^{-1} based on the bean (*Phaseolus vulgaris*) leaf respiration measurements of Amthor and Cummings [3]. Stem and root maintenance respiration rates ($\text{MRespRate}_{\text{Stem}}$, $\text{MRespRate}_{\text{Root}}$) were set to half the leaf rate based on the soybean (*Glycine max*) results of Kishitani and Shibles [20].

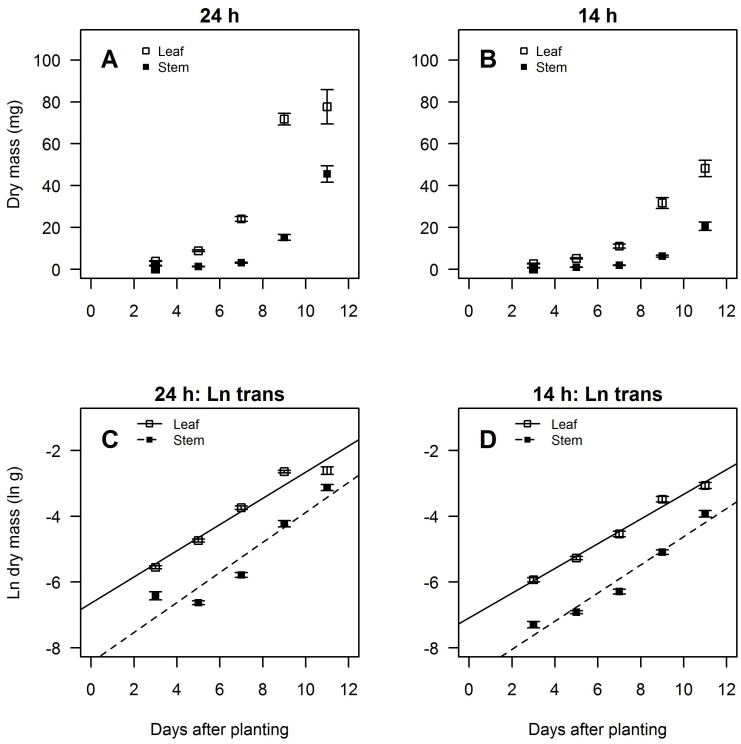


Figure 2: Measured (A, B) and logarithmically-transformed (C, D) leaf and stem dry mass for Wisconsin Fast Plants grown under 24 and 14 h illumination, for 10 plants on each harvest day under each growth condition. Lines represent linear regression of logarithmically-transformed leaf and stem dry mass against days since planting. Error bars represent standard errors of the mean.

The net photosynthetic rate (NetPsRate) was adjusted in 0.5 unit steps to the lowest value that satisfied leaf and stem potential demand under 24 h illumination. Using the parameters described here, a net photosynthetic rate of 8.5 μmol CO_2 m^{-2} s^{-1} met this criterion.

5.2. Comparison of simulated plant growth to measured plant growth under 24 h light

Using these parameters, simulated leaf and stem dry mass corresponded well to the measured values (Figure 3A,C,E). Measured and simulated values were log-transformed to homogenize variance and then the measured values were regressed on the simulated values [31]. The regressions explained 92 and 86% of the variation in leaf and stem dry mass, respectively. The slopes and intercepts of the regression lines for leaf and stem dry mass did not differ from 1 and 0, respectively, indicating that the simulation started, progressed, and ended with values near the measured values. Close correspondence of the measured and simulated values was expected because the model was developed using values obtained under 24 h illumination.

The net photosynthetic rate of 8.5 μmol CO_2 m^{-2} s^{-1} was somewhat less than the mean pho-

tosynthetic rate of 10.15 μmol CO_2 m^{-2} s^{-1} found for control *Brassica rapa* plants grown under a light intensity of 400 μmol m^{-2} s^{-1} [21]. As the light availability in the light boxes of our experiment was 282 μmol m^{-2} s^{-1}, a somewhat lower net photosynthetic rate appeared to be warranted.

5.3. Comparison of model results to measured values under 14 h light

Simulated leaf and stem dry mass for plants grown under 14 h illumination was 28 and 24% of the simulated values under 24 h illumination (Figure 3A,B). Simulated root dry mass under 14 h illumination was 9% of the simulated value under 24 h illumination. The simulated leaf and stem dry mass curves followed the trajectory of the measured values, but they were lower than the measured values at the end of the time period (Figure 3B,D,F). Regression of the measured values on the log-transformed simulated values explained 94 and 92% of the variation in leaf and stem dry mass, respectively, but the slopes of the lines were significantly greater than 1 and the intercepts were significantly greater than 0, because the simulated values underestimated the measured values. Thus, the simulated carbohydrate availability under 14 h illumination was not sufficient for leaves and stems to grow at the measured levels. From these results, we conclude that the hypotheses used to create the model were sufficient to explain the general pattern of growth but that the lack of full agreement occurred because at least one of the hypotheses was overly simplified. The use of constant potential RGRs to simulate leaf and stem growth is the most likely oversimplification in the model because we found significant deviations from linearity for the regression of log-transformed leaf and stem dry mass on time since planting for plants grown under 24 h illumination. In other systems, potential RGR is rarely constant. For example, peach vegetative potential RGR decreases rapidly early in the growing season and then remains constant for the remainder of the vegetative growth period [13] and peach fruit potential RGR is high following flowering, decreases over time by a factor of approximately 30, and then is relatively constant until fruit ripening [12]. Similarly, the potential growth rate of cucumber (*Cucumis sativus*) fruits changes over time [24, 25].

5.4. Sensitivity analysis

Sensitivity analysis is one way to assess the effect of various aspects of a model on the simulated outcomes; parameters that have disproportionate effects on model outcomes need to be characterized more fully than parameters that have little effect [17]. Models are considered to be "sensitive" to parameters for which a 10% change causes more than a 10% change in the state variables [17]. We found that changing leaf RGR by 10% under both 24 and 14 h illumination had large effects on leaf and total dry mass (Table 5). Similarly, under 14 h illumination , the model was sensitive to changing net photosynthetic rates by 10% (Table 5). These results illustrated the disproportionate, nonlinear effects of changes in leaf mass on carbon fixation and total mass accumulation as a result of the exponential nature of leaf growth. In contrast, decreasing the net photosynthetic rate by 10% under 24 h illumination decreased total mass by 10% but leaf mass by only 3% because, even with the decrease in photosynthetic carbon gain, sufficient carbon was available for the simulated plant to produce almost the same amount of leaf mass and area as it did under the initial conditions. We did not test the sensitivity of the model to a 10% increase in photosynthetic rate under 24 h

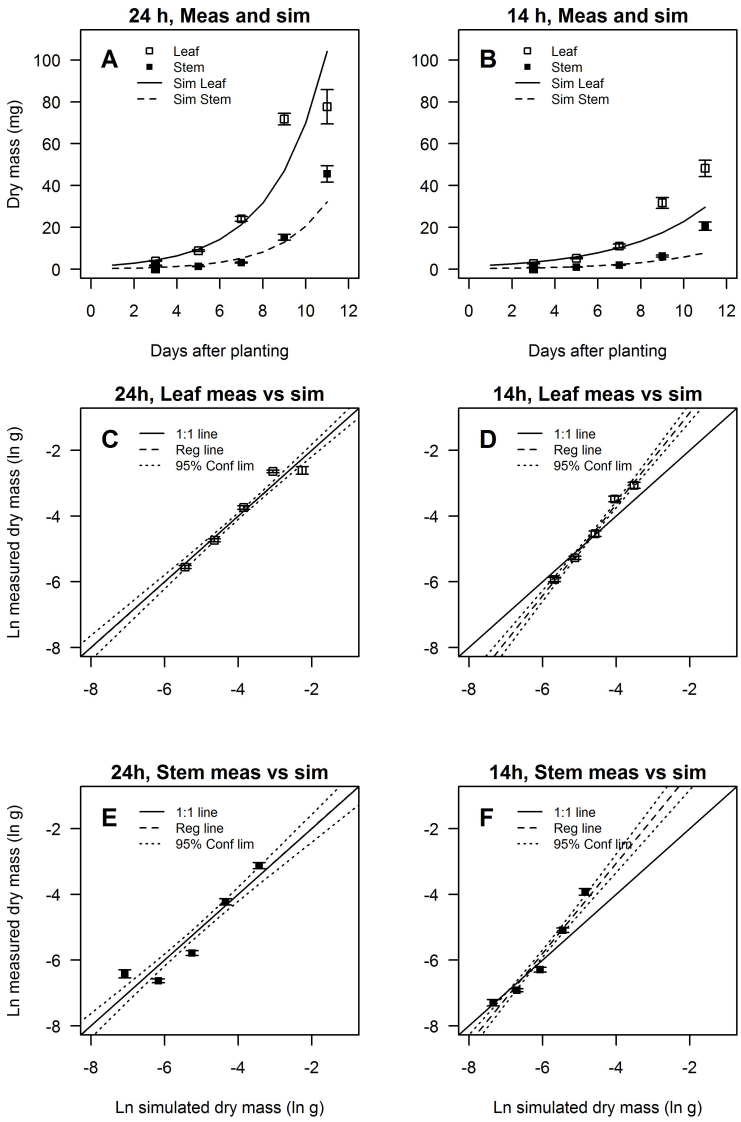


Figure 3: Measured (symbols) and simulated (lines) leaf and stem dry mass (A, B) versus days since planting for Wisconsin Fast Plants grown under 24 and 14 h illumination. Regression lines and 95% confidence limits for the regression are shown for measured vs. simulated logarithmically-transformed leaf and stem dry mass for Wisconsin Fast Plants grown under 24 (C, E) and 14 h (D, F) illumination. No significant deviations from a slope of 1 and intercept of 0 were detected for leaf or stem dry mass on plants grown under 24 h illumination. Slopes were significantly greater than 1 and intercepts were significantly greater than 0 for leaves and stems under 14 h illumination. Symbols represent means for logarithmically-transformed measured leaf and stem dry mass. Error bars represent standard errors of the mean.

illumination because simulated leaves and stems would have been growing at their maximum rates under this condition, and roots would have been the only compartment that could have received the additional carbohydrate that would have been produced with increased photosynthesis.

Increasing stem growth potential by 10% under both 24 and 14 h illumination shifted mass from leaves, whereas decreasing it shifted mass to leaves under 14 h illumination but had no effect under 24 h illumination. These results demonstrated the tradeoffs between leaves and stems when carbohydrate availability was limited although these shifts were not sufficient to change total biomass by more than 10%. Changing leaf, stem, and root respiration rates and root demand had little effect on plant growth, which indicated that accurately estimating these parameters was less important than estimating photosynthetic rate and potential leaf and stem RGR (Table 5).

Table 5: Percent change in simulated final leaf, stem, root, and total dry mass and total carbohydrate gain for simulated growth under 24 and 14 h illumination when leaf and stem potential RGR, root demand, net photosynthetic rate, and organ respiration rates were changed by 10%. Bold values indicate responses greater than 10%. The sensitivity of the model to a 10% increase in photosynthetic rate under 24 h illumination was not tested.

Growth condition and organ type	Leaf potential RGR		Stem potential RGR		Root demand		Net photosynthetic rate		Leaf, stem, and root respiration	
	+10%	-10%	+10%	-10%	+10%	-10%	+10%	-10%	+10%	-10%
24 h										
Leaf dry mass	**55**	**-36**	**-11**	0	0	0	–	-3	0	0
Stem dry mass	0	0	**44**	**-39**	0	0	–	-4	0	0
Root dry mass	**15**	**-28**	**-42**	**70**	0	0	**–**	**-61**	-1	1
Total dry mass	**39**	**-27**	-3	0	0	0	–	-10	0	0
14 h										
Leaf dry mass	**21**	**-21**	**-18**	**19**	-1	1	**27**	**-22**	-1	1
Stem dry mass	**-13**	**12**	**16**	**-19**	-1	1	**31**	**-24**	-2	2
Root dry mass	**-13**	**12**	**16**	**-19**	9	-9	**31**	**-24**	-2	2
Total dry mass	**13**	**-13**	-10	10	0	1	**28**	**-22**	-1	1

5.5. Summary of model performance

In summary, increasing the amount of carbohydrate available for plant growth by increasing photosynthetic rate and leaf potential growth rate increased total biomass accumulation (Table 5). These results parallel the effects of increasing nitrogen availability through fertilization, which increases leaf level photosynthetic rates [22] and produces "leafy" plants with small root systems and a high shoot-to-root ratio [33]. Increasing leaf dry mass by increasing leaf potential RGR or decreasing stem potential RGR in the model increased the proportion of carbon partitioned to leaves, leaf area, and total dry mass (Table 5). In general, fast growing species partition a greater amount of carbon to leaves than slow growing species and, as a result, gain relatively more carbon on a whole plant basis [22, 32]. For example, during the Green Revolution, rice and wheat breeders reduced

stem RGR by developing dwarf varieties that partitioned less of their carbon to stems and more to the harvested portion of the plant compared to older varieties [19]. Similar explorations of the relationships among the processes of photosynthesis, energy, and water use may be conducted in PlantMod, an interactive model of the physiology of plant canopies [18].

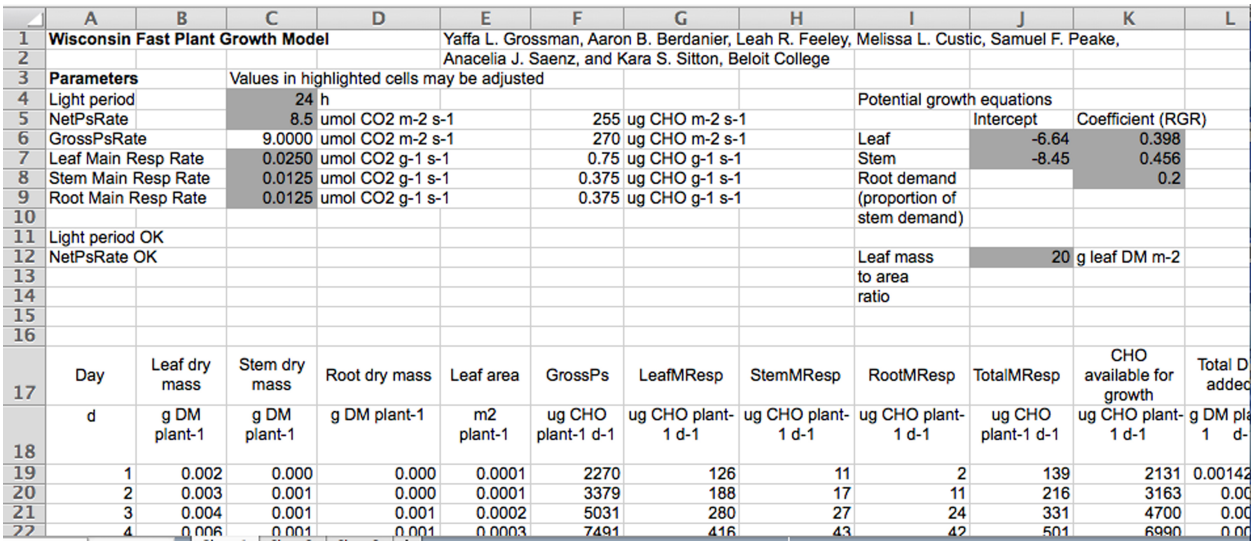
The greatest weakness of the model is its treatment of roots as the "overflow" compartment for carbohydrate in excess of leaf, stem, and root potential demand (Figure 1). Our model shares this weakness with many other plant growth models; LeRoux et al. [23] noted that below-ground processes are absent from most of the 27 models of individual tree growth they examined.

6. Student responses to the modeling project

The plant ecophysiology course included a wide range of discussions and laboratory activities, but most of the responses on the course evaluation at the end of the semester addressed the modeling experiment and related activities. The evaluations included comments such as "I really enjoyed the modeling framework and think that it is a valuable skill to have, both immediately and long-term." and "Modeling plant growth isn't easy but we were able to understand and work with valuable tools essential for the future." Students also reported that learning to use Excel more thoroughly, working with equations, and manipulating the model were helpful.

7. Future uses of the model

Students and others may use the equations included in this study to implement their own models of vegetative growth using Wisconsin Fast Plants or other species. In addition, the Wisconsin Fast Plant Growth Model itself is available (Figure 4, BioQUEST curriculum Consortium (http://bioquest.org/esteem/materials) and may be used to explore the effects of changing the model parameters. Although model users might not develop the same level of understanding as the model developers, the model should help users improve their understanding of the carbon economy of plants [9, 27]. For example, during the spring semester of 2010, students in a plant ecophysiology course taught at Beloit College by one of us (ABB) performed a laboratory exercise in which they received a brief introduction to the model followed by an invitation to identify at least one ecological or physiological variable that they could manipulate with it. They made qualitative predictions about how a plant would respond to their manipulation, modified the Excel spreadsheet to simulate this change, compared the control version of the model to the outcome of their manipulation, and then discussed whether the changes they observed were realistic and fit with their knowledge of plant ecophysiology. This process stimulated a lively discussion about the relationships among leaf area, photosynthetic and respiration rates, and carbon acquisition. Such a conversation could be used to set the stage for seminar discussions about contemporary issues that involve the carbon economy of plants, such as the interactions among photosynthetic rate, fertilization, leaf area development and crop yield [41]; calculation of the amount of carbon absorbed by forests [4]; and the differences in harvestable biomass produced by different types of biofuel crops [6]. Such conversations help promote integrated learning of the type emphasized by recent reports on science



	A	B	C	D	E	F	G	H	I	J	K	L
1	**Wisconsin Fast Plant Growth Model**				Yaffa L. Grossman, Aaron B. Berdanier, Leah R. Feeley, Melissa L. Custic, Samuel F. Peake,							
2					Anacelia J. Saenz, and Kara S. Sitton, Beloit College							
3	**Parameters**		Values in highlighted cells may be adjusted									
4	Light period		24	h					Potential growth equations			
5	NetPsRate		8.5	umol CO2 m-2 s-1		255	ug CHO m-2 s-1			Intercept	Coefficient (RGR)	
6	GrossPsRate		9.0000	umol CO2 m-2 s-1		270	ug CHO m-2 s-1		Leaf	-6.64	0.398	
7	Leaf Main Resp Rate		0.0250	umol CO2 g-1 s-1		0.75	ug CHO g-1 s-1		Stem	-8.45	0.456	
8	Stem Main Resp Rate		0.0125	umol CO2 g-1 s-1		0.375	ug CHO g-1 s-1		Root demand		0.2	
9	Root Main Resp Rate		0.0125	umol CO2 g-1 s-1		0.375	ug CHO g-1 s-1		(proportion of			
10									stem demand)			
11	Light period OK											
12	NetPsRate OK								Leaf mass	20	g leaf DM m-2	
13									to area			
14									ratio			
15												
16												
17	Day	Leaf dry mass	Stem dry mass	Root dry mass	Leaf area	GrossPs	LeafMResp	StemMResp	RootMResp	TotalMResp	CHO available for growth	Total D added
18	d	g DM plant-1	g DM plant-1	g DM plant-1	m2 plant-1	ug CHO plant-1 d-1	ug CHO plant-1 d-1	ug CHO plant-1 d-1	ug CHO plant-1 d-1	ug CHO plant-1 d-1	ug CHO plant-1 d-1	g DM pl 1 d-
19	1	0.002	0.000	0.000	0.0001	2270	126	11	2	139	2131	0.00142
20	2	0.003	0.001	0.000	0.0001	3379	188	17	11	216	3163	0.00
21	3	0.004	0.001	0.001	0.0002	5031	280	27	24	331	4700	0.00
22	4	0.006	0.001	0.001	0.0003	7491	416	43	42	501	6990	0.00

Figure 4: Screen shot of Wisconsin Fast Plant Model implemented in Microsoft Excel®. Highlighted fields indicate parameters that users may adjust.

education [1, 29].

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Appendix 1
Calculation of the potential demand for plant dry matter by each organ type

To calculate the potential growth for leaves, stems, and roots on one day, we used the exponential growth equation ($A_t = A_0 e^{rt}$) with the current dry mass of the organ ($\text{Mass}_{\text{Organ}}$) for A_0, the potential RGR for the organ ($\text{PotRGR}_{\text{Organ}}$) for r, and t=1 and then subtracted the current dry mass of the organ:

$$\begin{aligned}\text{PotDemand}_{\text{Organ}} &= \text{Mass}_{\text{Organ}} * e^{\text{PotRGROrgan}*1} - \text{Mass}_{\text{Organ}} \\ &= \text{Mass}_{\text{Organ}} * (e^{\text{PotRGROrgan}} - 1)\end{aligned}$$

This equation calculates the potential interest (potential demand) earned over one time interval on the initial capital (initial dry mass).