

A validated mechanistic model of carrot (*Daucus carota* L.) growth

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ABSTRACT

A mechanistic model of carrot vegetative and root development was constructed. This model determined canopy photosynthesis over a day, assimilates were then partitioned into either roots or leaves via temperature dependent partitioning coefficients. Assimilates were lost via terms describing growth and maintenance respiration. The model was calibrated on data from four different carrot cultivars, originating from the UK (Autumn King), Syria (Carrot_S), Poland (Dolanka) and Russia (Hibinskaja), grown in controlled environment glasshouse compartments at one of six temperatures (9–30 °C) repeated over three sowing dates. Calibration of the model showed that it could account for between 83 and 95% of the variance in carrot plant and root dry weights. The model was then validated using independent data from the same cultivars of carrots grown in the field at Reading. In this instance, the model accounted for 75 and 79% of the variance in plant and root weight, respectively. Two other independent data sets were used to validate the model, including carrot of a different cultivar (Panther) grown in phytotrons at temperatures between 9 and 21 °C, at two different locations and over a three sowing dates. In this instance, the model accounted for between 63 and 69% of the variance in root weight. The model also predicted that if ambient carbon dioxide levels increased from 348 to 551 $\mu\text{mol mol}^{-1}$, root dry weight would increase by 12%, which is within the margin of error of the experimental value of 16% reported in the literature. The model can therefore be used to study the potential impacts of global climate change on carrot production, as well as to rapidly predict whether germplasm is suited to any particular environment.

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1. Introduction

An accurate quantitative description of the factors affecting carrot growth would be of considerable value to growers as a decision support tool. Accurate decision support systems can be used to assist growers with crop scheduling, forecasting and optimisation of root quality and growth. They also give a more thorough understanding of the factors that may influence the crop (Pearson et al., 1997), and may provide a basis to determine whether a genotype is suited to a particular environment. To date, as far as we are aware, there have been no attempts to construct a mechanistic model of carrot growth. The objective of this study was “to construct a model of carrot growth”, from the methods “using an extensive data set” from a study on the genotypic and environmental regulation of carrot growth (Hussain, 1999).

2. Materials and methods (theory)

The quantitative framework was developed from an original lettuce growth model described by Sweeney et al. (1981). Their model assumed that lettuce dry matter was produced from photosynthesis and converted into one of two pools of dry matter, either storage or structural. The rate of conversion from storage to structural dry matter was dependent upon temperature and the size of the total carbon pool. A fixed leaf area ratio was assumed, thus leaf area expanded in proportion to the size of the structural dry matter pool. The proportion of light intercepted by the canopy was determined from an adapted form of the Monsi-Saeki equation. Dry matter was lost via respiration, and canopy photosynthesis was assumed to decrease as an exponential function of time.

The lettuce model was subsequently adapted by Pearson et al. (1997) in an analysis of the potential impacts of climate change on the growth of lettuce crops in the UK. The main adaptations to the model were that rate of decrease of canopy photosynthesis was a function of thermal time, the function predicting canopy photosynthesis was converted to be dependent upon ambient carbon

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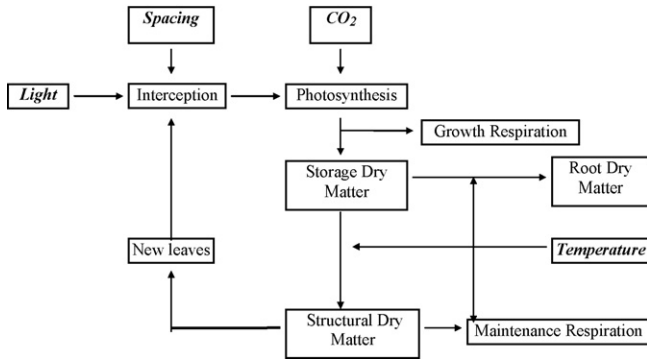


Fig. 1. A schematic diagram that shows the processes modelled to predict the growth of carrot.

dioxide concentration and that the conversion from storage to structural dry matter was changed to become proportional to temperature and the size of the storage pool. This model was validated using seven independent data sets. It has subsequently been applied to predict growth and flowering of New Guinea Impatiens (Smith and Pearson, unpublished).

The essence of the model of carrot growth described here is similar to those proposed by Sweeney et al. (1981) and Pearson et al. (1997) however, there are a number of key alterations. A framework for the model is shown in Fig. 1. Carbon is fixed via canopy photosynthesis, it then moves to one of three pools, either storage, root or structural dry matter. The rates of conversion between the pools are related to temperature by partitioning constants.

The proportion of light intercepted by the canopy (Q) was taken from a modified form of the Monsi-Saeki equation and was adapted from Sweeney et al. (1981), where

$$Q = \frac{1}{h} (1 - e^{-kF_v W_v h}) \quad (1)$$

h is the plant density (distance between plants assuming square planting arrangement), F_v is the structural leaf area ratio (LAR) ($\text{m}^2 \text{kg}^{-1}$), W_v is the vegetative (structural) dry matter (kg), and k is the canopy extinction coefficient. F_v was assumed to be $135 \text{ m}^{-2} \text{kg}^{-1}$. The value of the extinction coefficient used represents a canopy with totally random leaf angle distribution (Monteith and Unsworth, 1990).

Daily canopy photosynthesis (∇c , $\text{kg}(\text{CO}_2) \text{ plant}^{-1} \text{ d}^{-1}$) was determined using an analytical relationship developed by Charles-Edwards et al. (1986) for spaced plants, ideal for a horticultural crop, where

$$\nabla c = \left[\frac{\alpha S A_m d Q}{(k\alpha S + dA_m)} \right] - \nabla_R \quad (2)$$

α is leaf light use efficiency ($\text{kg}(\text{CO}_2) \text{J}^{-1}$), S is the daily PAR (photosynthetically active radiation) light integral (J) measured above the canopy, A_m is the maximum rate of leaf photosynthesis for a light saturated leaf ($\text{kg}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$), d is the duration of the photoperiod (s) and ∇_R is the daily respiratory integral. This relationship assumes a rectangular hyperbolic relationship between irradiance and photosynthetic rate. It also assumes that irradiance varies according to a sinusoidal relationship over a day.

To consider effects of varying carbon dioxide concentration, α was adjusted according to the empirical relationship provided by Pachepsky et al. (1994), for cotton, where

$$\alpha_{\text{CO}_2} = \alpha + \left(\frac{0.2\alpha}{C} \right) (C_a - C) \quad (3)$$

α_{CO_2} is the CO_2 dependent light use efficiency, C is a reference CO_2 concentration ($0.000622 \text{ kg}(\text{CO}_2) \text{ m}^{-3}$) and C_a is the ambient concentration ($\text{kg}(\text{CO}_2) \text{ m}^{-3}$).

Rate of canopy photosynthesis was also assumed to be dependent upon the ambient temperature. The model adjusted the rate of canopy photosynthesis using a symmetrical relationship, which decreases the rate proportionally above and below a fixed optimum T_{op} . The advantage of this approach is that the model can be calibrated with a single parameter, the optimum temperature for maximum rate of photosynthesis (T_{op}). The approach is similar to the effective temperature concept used by Pearson et al. (1993) to model flowering in Chrysanthemums, thus:

$$A_{\text{pt}} = \frac{T_{\text{op}} - |T_a - T_{\text{op}}|}{T_{\text{op}}} \quad (4)$$

where A_{pt} is the proportionate reduction in photosynthetic rate with temperature, T_a is the average air temperature.

Photosynthesis was also assumed to decline with age, though as a function of thermal rather than chronological time, as also used by Pearson et al. (1997), thus

$$A_{\text{pl}} = \frac{\theta_m - \theta_i}{\theta_m} \quad (5)$$

where A_{pl} is the proportional reduction in photosynthetic rate with thermal time, θ_m is the thermal time accumulated above a base temperature of 0°C at which point photosynthetic rate is zero, θ_i is the thermal time accumulated from sowing on day i .

Dry matter was assumed to be lost through ∇_R respiration, where according to McCree (1970):

$$\nabla_R = a_0 \nabla c + a_1 W \quad (6)$$

where $a_0 \nabla c$ is the growth respiration and $a_1 W$ is the maintenance component. W is the total plant dry mass ($W_G + W_v + W_R$) and a_0 and a_1 are constants.

Assimilates produced from photosynthesis were assumed to enter initially the storage dry matter pool of mass (W_G). These were then converted into either vegetative (structural, W_v) or root (W_R) dry matter, where the rate of conversion was given by:

$$\frac{dW_v}{dt} = W_v P_v T_a \quad (7)$$

and

$$\frac{dW_R}{dt} = (W_G + W_v) P_R (T_{\text{or}} - |T_{\text{or}} - T_a|) \quad (8)$$

where P_v and P_R are temperature dependent partitioning coefficients ($\text{kg kg}^{-1} \text{ d}^{-1} \text{ }^\circ\text{C}^{-1}$). No temperature optima were assumed for the rate of vegetative dry matter partitioning, but for root, the rate was constrained about an optimum temperature, T_{or} , again using a simple effective temperature function. Rate of root development in Eq. (8) was assumed to be dependent upon the overall size of both the stored and structural carbohydrate pools. Through Eq. (1), the production of new vegetative dry matter then increases total plant leaf area, and therefore light interception.

The use of the analytical solution to daily rate of canopy photosynthesis made the model relatively simple to solve with a time step of 1 day, and the rate of change of size of the storage carbon pool can be summarised, with some rearrangement, as follows:

$$\frac{dW_G}{dt} = \frac{\psi}{h} \frac{1 - e^{-kF_v W_v h}}{(k\alpha_{\text{CO}_2} S + dA_m) A_{\text{pt}} A_{\text{pl}} (1 - a_0)} - a_1 (W_G + W_v + W_R) - \frac{dW_v}{dt} - \frac{dW_R}{dt}$$

where ψ is a factor to convert CO_2 into hexose.

Table 1
Parameter definitions and values used in the mechanistic carrot model

Parameter	Definitions	Values for four carrot cultivars				Search range (increment)	References
		Carrots _s	Hibinskaja	Dolanka	Autumn King		
K	Extinction coefficient	0.42	0.42	0.40	0.42	0.4–0.6 (0.02)	
ψ	Factor to convert CO ₂ to plant dry weight	30/44	30/44	30/44	30/44		
h (m)	Distance between plants	0.0153	0.0153	0.0153	0.0153		
F_v (m ⁻² kg ⁻¹)	Leaf area ratio (LAR)	135	135	135	135		Estimated from Hussain (1999)
α_m (kg(CO ₂)J ⁻¹)	Leaf light utilisation efficiency	1.40E-08	1.40E-08	1.45E-08	1.40E-08	1.2–1.6 (0.05E-08)	Sweeney et al. (1981)
(m s ⁻¹)	Leaf conductance	0.002	0.002	0.002	0.002		Sweeney et al. (1981)
C (kg(CO ₂) m ⁻³)	CO ₂ concentration	0.000622	0.000622	0.000622	0.000622		Sweeney et al. (1981)
θ_m (°C d)	Thermal time for the cessation of photosynthesis	5100	5100	5100	5100		
θ_l (°C d)	Thermal time on day _l						
S (J d ⁻¹)	Horizontal irradiance above the canopy (PAR)						
T_{op} (°C)	Optimum temperature for photosynthesis	18.5	19.0	18.0	19.0	15–20	
T_{or} (°C)	Optimum temperature for root partitioning	16.5	19.0	17.0	17.0	15–20	
P_v (kg kg ⁻¹ d ⁻¹ °C ⁻¹)	Temperature dependent vegetative partitioning coefficient	0.0020	0.0017	0.0022	0.0023	0.001–0.003 (0.0001)	
P_R (kg kg ⁻¹ d ⁻¹ °C ⁻¹)	Temperature dependent root partitioning coefficient	0.0040	0.0037	0.0032	0.0034	0.002–0.005 (0.0001)	
A_m (kg(CO ₂) m ⁻² s ⁻¹)	Maximum rate of leaf photosynthesis for light saturated leaf	0.0005	0.0005	0.0005	0.0005		Charles-Edwards et al. (1986)
a_0	Growth respiration rate	0.26	0.20	0.20	0.20	0.16–0.30 (0.02)	McCree (1970)
a_1	Maintenance respiration rate	0.040	0.030	0.022	0.030	0.02–0.04 (0.001)	McCree (1970)

Parameters in bold were fixed, others were fitted.

3. Results

3.1. Fitting the model

Due to the large number of variates, a systematic grid search procedure was used to fit the model, whereby the values of the parameters were adjusted, within physiologically acceptable limits (Table 1), until model predictions converged with the actual data (i.e. the residual sum of squares between the predicted and actual plant mass were minimised). A similar procedure was also used by Sweeney et al. (1981) and Pearson et al. (1997). The starting values (initial plant dry weight) assumed initially that the dry matter comprised of 95% structural (vegetative) and 5% storage dry mass.

3.2. Model calibration

The data used to calibrate the model were taken from an extensive series of experiments on carrot growth in semi-controlled environment facilities (Hussain, 1999). Four different cultivars of carrot were grown for 91 days from three sowing dates (winter, spring and summer) at each of six temperatures ranging between 9 and 30 °C. The varieties grown were Carrots_s (Syrian), Hibinskaja (Russian), Dolanka (Poland) and Autumn King (UK). All were obtained from the Vegetable Genebank of Horticulture Research International (HRI), Wellesbourne. Daily light integral and temperature were collected on site. The average daily temperature and daily light integral recorded each day were used as the driving variables, and the model was integrated with a time step of 1 day. The daily photoperiod, one of the input variables to the model was estimated from astronomical equations (Seller, 1965).

There was a good model agreement between the predicted and actual root and plant mass for all four cultivars (Figs. 2 and 3). The coefficients of determination were between 0.83–0.90 ($P > 1\%$) and 0.87–0.95 ($P > 1\%$) for root and plant mass, respectively. The coefficients used to parameterise the model are shown in Table 1. They were remarkably similar between varieties; however, due to

the complexity of the model it was not possible to determine statistical error values for the coefficients. The values for the optimum temperatures for partitioning are consistent with those reported by Hussain (1999). The main difference between cultivars was in the value of the partitioning coefficients from storage to root and structural dry matter. In a previous study, (Hussain, 1999) carrot cultivars demonstrated dramatic variations in partitioning between roots and vegetative components.

3.3. Model validation

Independent data sets from six field grown crops of carrot were used to test the validity of the model. Crops of each cultivar, used for model calibration, were grown as part of a large germplasm characterisation experiment conducted at Reading during 1995 and 1996 (Hussain, 1999). In each year, carrots were sown on three occasions (March, April and May) and harvested after 101 days of growth. Therefore, there were data on six crops for each cultivar. The model was validated using all parameter values derived from the calibration crops. The values predicted by the model were a good fit to the data (Fig. 4) [$r^2 = 0.75$ ($P > 1\%$), d.f. 23 for plant dry weight, $r^2 = 0.79$ ($P > 1\%$), d.f. 23 for root dry weight]. There was slight evidence for an over prediction of plant dry weight (less for root dry weight) at higher values, however, most of the error bars for individual points intersected the line of identity, suggesting a good fit largely within the variance associated with an individual data point.

A second series of independent model validations were conducted with data reported by Rosenfeld et al. (1998a,b). In the first instance (Rosenfeld et al., 1998a), carrots were grown in phytotrons at one of five temperatures between 9 and 21 °C, and at each of two sites Ås and Tromsø. Roots were harvested on each of two occasions during growth, and fresh weight as well as percentage dry matter was reported. Their data set showed that the optimum temperature for maximum root weight to cv. Panther was lower than that found for any of the varieties studied here (approx. 12–15 °C compared to 16–19 °C). Therefore, the model

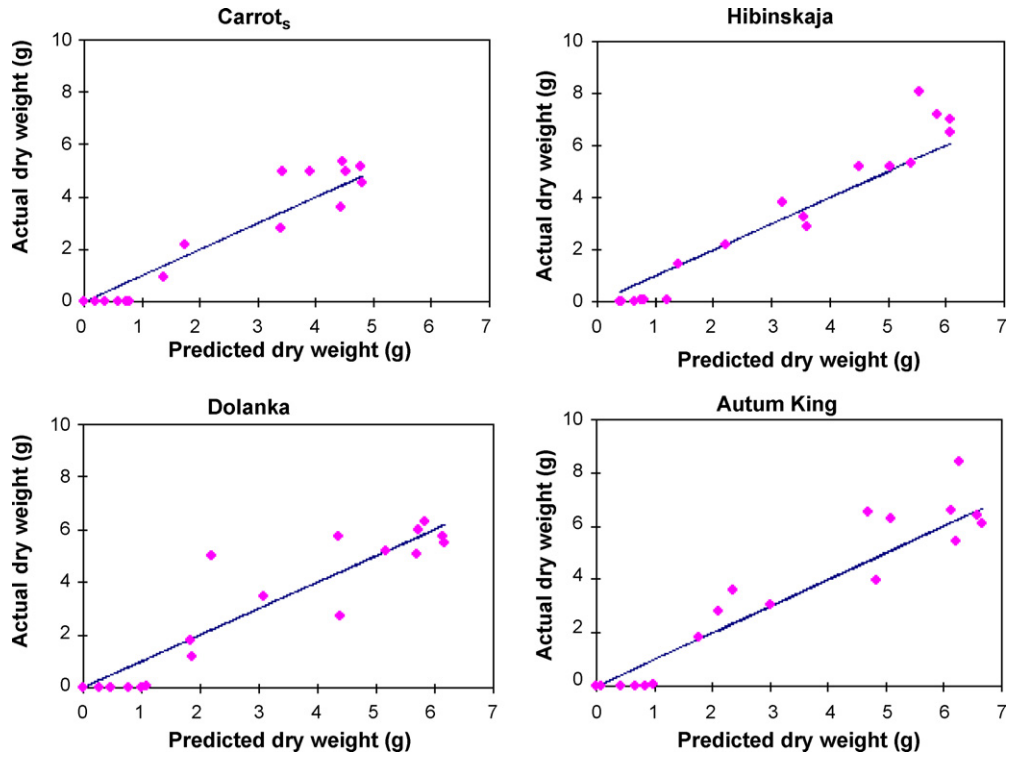


Fig. 2. The relationship between the actual root dry weights and those predicted by the model for calibration for four carrot cultivars, where r^2 and d.f. for root dry weight for Carrot_s (0.83*, 15), Hibinskaja (0.90*, 17), Dolanka (0.85*, 17) and Autumn King (0.89*, 17). The line represents, the line of identity (1:1). * Refers to significance at >1% probability level.

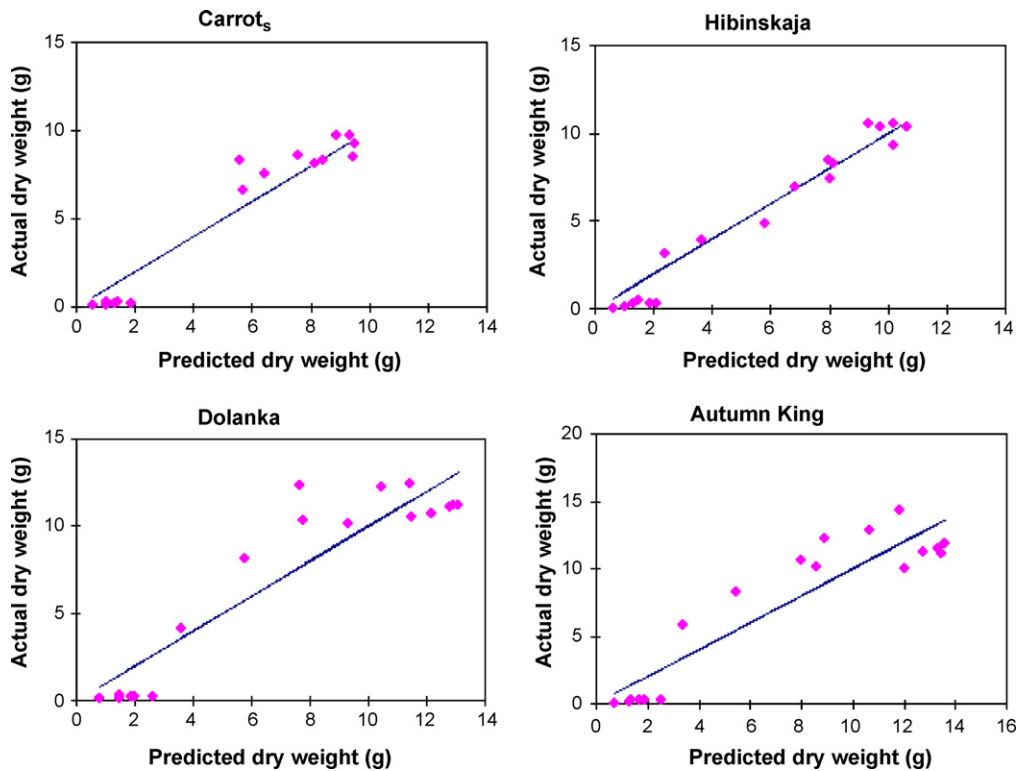


Fig. 3. The relationship between the actual plant dry weights and those predicted by the model for calibration for four carrot cultivars, where r^2 and d.f. for plant dry weight for Carrot_s (0.87*, 15), Hibinskaja (0.95*, 17), Dolanka (0.86*, 17) and Autumn King (0.85*, 17). The line represents, the line of identity (1:1). * Refers to significance at >1% probability level.

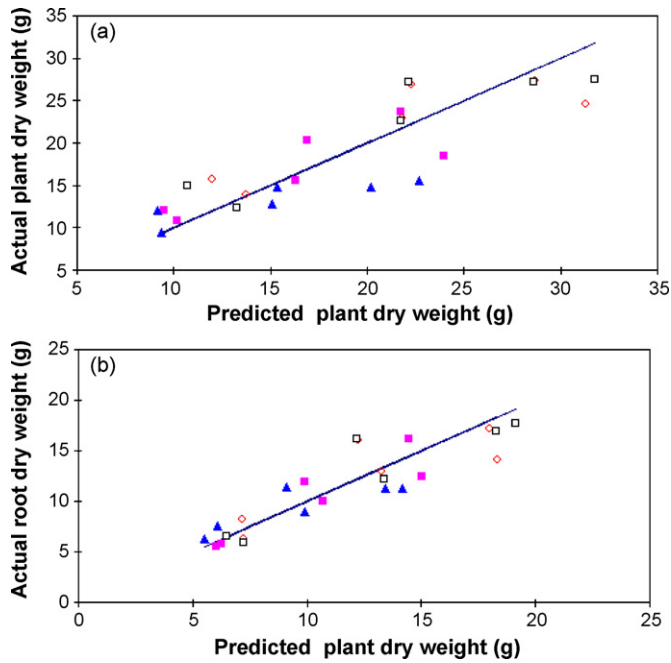


Fig. 4. The relationship between the actual plant (a), root (b) dry weights and those predicted by the model for validation for cultivars Carrots (■), Hibinskaja (▲), Dolanka (○), and Autumn King (□), where r^2 and d.f. for plant dry weight (0.75*, 23) and for root dry weight (0.79*, 23). * Refers to significance at >1% probability level.

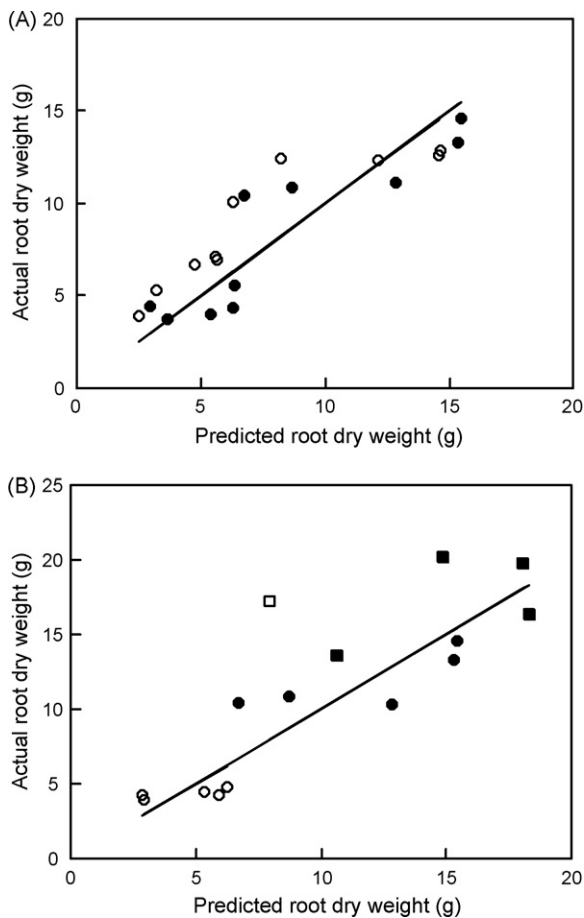


Fig. 5. A validation of the model, predicted root dry weights compared to those measured experimentally at two sites Ås and Tromsø (A) by Rosenfeld et al. (1998a) and with three sowing dates 21 September, 21 March and 26 June at one location Ås (B) for cv. Panther Rosenfeld et al. (1998b).

was run for the purposes of the validation with the optimum temperature root partitioning (T_{or}) set at 12 °C. All other parameter values were as determined for the variety Autumn King (see Table 1). All the meteorological data required were reported by the authors. The model gave a good description of root dry weight ($r^2 = 0.63$), despite the fact that this variety was not studied during model calibration (Fig. 5A).

A second independent validation was conducted using data from Rosenfeld et al. (1998b). In this instance, carrot (cv. Panther) was grown in phytotrons at the same temperatures reported in Rosenfeld et al. (1998a), but using three sowing dates throughout the year (21 September, 21 March, 26 June), though at only one location (Ås). The model gave a good fit to the data (Fig. 5B). In this instance, one point was a significant outlier (9 °C, sown 26 June), however, when removed from the analysis the model accounted for 69% of the variance in root weight. It is not, however, possible to determine whether the unaccounted variance was attributable to variance associated with each data point (pure error) or real lack of fit, since Rosenfeld et al. (1998a,b) did not report individual standard errors of the data.

Data reported by Wheeler et al. (1994), for carrots grown in a field based thermal gradient chamber at 348 and 551 $\mu\text{mol mol}^{-1}$ CO_2 , were used to test whether the model could simulate the impacts of increased carbon dioxide levels on carrot growth. The model was run using the parameter values for cv. Autumn King (Wheeler et al., used cv. Primo) and ambient meteorological data for Reading during the experimental period. At ambient carbon dioxide levels and a mean temperature of 9 °C, the model predicted a dry weight of 3.4 g compared to approx. 3.6 reported by Wheeler et al. (1994). When carbon dioxide level was increased to 551 $\mu\text{mol mol}^{-1}$ dry matter was predicted to rise by 12%, compared to 16% reported experimentally by Wheeler et al. (1994). This is largely within the margin of experimental error and therefore the model seems to have potential to predict the impacts of climate change on carrot growth.

3.4. Simulation

To illustrate the potential effects of changes to the environment on plant dry weight, the model was run with the parameter values for cultivar Autumn King (Table 1). There was a relationship between plant dry weight with systematic changes in temperature and PAR (Fig. 6). It suggests that small temperature increases were simulated to substantially increase of plant dry weight up to an

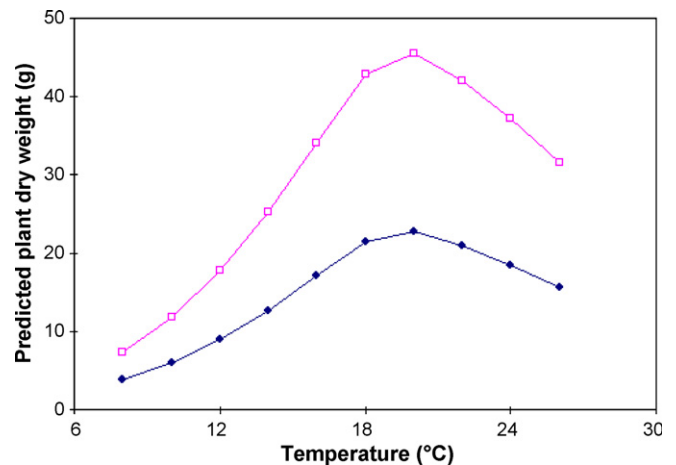


Fig. 6. A simulation of the effect of temperature (8–26 °C) and PAR [$6 \text{ MJ m}^{-2} \text{ d}^{-1}$ (■), $12 \text{ MJ m}^{-2} \text{ d}^{-1}$ (□)] on the plant dry weight of carrot cultivar Autumn King grown for 91 days.

optimal temperature (20 °C), and further increase in temperature decreased the plant dry weight (Fig. 6). Whilst when PAR doubled, plant dry weight was almost two-fold higher at all temperature levels. The change in solar radiation did not affect the optimum temperature, so that at both lower and higher PAR levels the highest total biomass was observed at the same temperature (20 °C).

4. Discussion

This study has produced a comprehensive model of the effects of environment on the root and plant growth of carrot. The model is analogous to that provided by Pearson et al. (1997), the main differences being that respiration was divided into growth and maintenance components and a third 'root' carbon pool was added. These improve the physiological 'robustness' of the model, and obviously reflect differences between lettuce and carrot crops. The model is relatively simple and therefore capable of solution with minimal computational effort.

The model provided an excellent fit to a substantial calibration data set. This calibration data set is rather unusual in terms of model construction, in that it encompasses data from plants grown in diverse temperature and light integral combinations. Such an extensive calibration data set is essential for a model that may be used for commercial decision support, since it must have the capability to forecast the growth of crops grown in a wide range of environments.

The model was independently validated on four data sets, one from carrots grown in the field, two from phytotrons experiments and one from data from a thermal gradient experiment. In all cases the model gave a reasonable fit to the data, despite the fact that different varieties were used in three of the four data sets. This suggests that the model is robust and provides a reasonable description of carrot physiology. Of notable interest the model seemed to provide a reasonable demonstration of the effects of enhanced levels of carbon dioxide on carrot growth. Thus, it has potential to predict the impacts of climate changes on carrot production. A similar version of the model, but calibrated for lettuce, was used for this purpose by Pearson et al. (1997).

One of the features of the carrot is that it is very sensitive to temperature (see Rosenfeld et al., 1998a,b; Hussain, 1999), as demonstrated with the data presented here. This is usually a weakness in many mechanistic models, which often place great emphasis on accurately predicting canopy assimilation rather than temperature sensitivity. High sensitivity to temperature was achieved in this model by using a simple relationship between leaf photosynthesis and temperature, and by changing the temperature optima for root and plant partitioning.

The robustness of the calibration procedure suggests that the model has potential application. This study has a number of implications for practical carrot production and the relationships reported here may be applied by the growers in a number of ways.

For example, the model could be used to predict optimal environmental requirements for crop growth and also to predict crop yield. The model could be used to develop improved sowing date schedules. Furthermore, the model might be used by the growers as a predictive tool, to indicate how to change the environments (e.g. carrot production under plastic covers) advance or delay the rate of growth in accordance with market demands and quality requirements.

Models have a role in germplasm screening. Economically it might not be worth testing each cultivar at different locations to decide how a particular cultivar will perform. However, via this model, in conjunction with meteorological data of any location, growth and yield for a particular cultivar can be predicted for rapid germplasm screening to determine whether an environment is suited for carrot growth per se.

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