Agricultural Water Management 232 (2020) 106066

Contents lists available at ScienceDirect

Agricultural Water Management

journal homepage: www.elsevier.com/locate/agwat

Simulation of plant height of winter wheat under soil Water stress using modified growth functions

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ARTICLE INFO

Keywords:
Winter wheat
Water stress
Growth function
Plant height
Crop modeling

ABSTRACT

Plant height is an important trait that influences the yield and sustainability of wheat productions. It is also an important objective for agronomic breeding and a critical indicator to represent the status of crop growth and nitrogen absorption in the vegetative stage. Wheat is the main crop in arid regions. However, there is insufficient understanding of wheat plant height response to soil water stress. In this study, we tried to explore a new algorithm for simulating dynamics of winter wheat height under different scenarios of soil water stress based on soil column and field experiments conducted under rainout shelters between 2012 and 2016 at Yangling, Shaanxi province, China. First, we established a temperature response function of wheat plant height based on four cardinal temperatures (i.e. base temperature, lower optimal temperature, higher optimal temperature, and ceiling temperature). And we also constructed a water stress response function of wheat plant height using relative soil water availability (A_w) as water stress index. Then, these two functions were used as multipliers to modify the first-order derivative of six distinct growth functions (i.e. Gompertz, Logistic, Mischerlich, Richards, Von Bertalanffy, and Weibull) to represent the elongation rate of wheat plant height under soil water stresses. Consequently, six modified simulation models for wheat plant height were established and identified as Mod-Geo, Mod-Log, Mod-Mis, Mod-Ric, Mod-Von, and Mod-Wei, respectively, among which an optimal simulation model was selected for winter wheat growth under soil water stresses. Based on experimental data of 2014–2015 used for model calibration, it was found that when A_w was greater than 0.65, elongation rate of wheat height was not influenced by soil water content; when A_w was between 0.3 and 0.65, elongation rate of wheat height gradually reduced following an exponential function driven by water stress; when A_w was less than 0.30, elongation rate of wheat height rapidly and linearly reduced driven by water stress until A_w was close to 0 at which the elongation stopped. After that, the data of soil column experiment of 2014–2015 growing season were used to assess the parameters of the six newly established models. The results of model calibration showed that the mean value of the Willmott Index of Agreement (WIA) between measured and simulated wheat heights of the six cultivars were all less than 0.90 for all treatments in the experiment, except for the Mod-Log model (0.95). The data of soil column experiment in 2015–2016 seasons were used to validate the six calibrated new models. The results of model validation with mean value of WIA 0.93 which were even better than model calibration. Finally, the data of two growing seasons (2012–2013 and 2013–2014) of field experiments conducted under a giant rainout shelter were used for further verification of the six new models under field conditions. Among the six different plant height simulation model, Mod-Log model obtained the best values of RMSE and WIA.

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https://doi.org/10.1016/j.agwat.2020.106066
Received 17 September 2019; Received in revised form 29 January 2020; Accepted 1 February 2020
0378-3774/

1. Introduction

Plant height, as an important index to reflect crop growth and nitrogen absorption in vegetative stage, is an important character affecting yield of wheat and other crops. It is also an important trait of crop breeding (Yao et al., 2011). Besides, plant height is one of the major driving factors in modeling yield loss due to lodging (Berry et al., 2003; Sterling et al., 2003). Baker et al. (1998) simulated wheat lodging and found that the variation of gravity center of wheat height influence wheat lodging risk. Plant height simulation is also important for the three-dimensional construction of crop canopy structure (Burgess et al., 2015). Additionally, crop plant height is an indispensable variable for simulating crop intercropping systems, as it is one of the main factors that affect the ability of the crop light interception (Guénaëlle et al., 2009).

However, models simulating crop plant heights were rarely developed and used in the last decades. Some widely-used models, such as the CERES family models (Ritchie et al., 1988), ignored plant height simulations since they considered canopy as a monolayer when simulating the light interception (Confalonieri et al., 2011).

Recently, the importance of plant height in modeling canopy micrometeorology was gradually recognized by researchers (Fang et al., 2014). Fang et al. (2014) coupled a plant height model with the revised RZ-SHAW model and improved the accuracy of simulations of evapotranspiration and energy balance in a wheat–maize cropping system. Furthermore, some simple methods have been proposed to simulate plant height. Lizaso et al. (2005) described the corn plant height as the final function driven by maximum plant height and development stage. Kotera and Nawata (2007) presented a plant height simulation method in a rice model driven by average daily temperature, plant height of the day before, and maximum plant height. Another method based on LAI was implemented in CropSyst model (Bechini and Stöckle, 2007). Among these crop plant height simulation models, the Lizaso et al. (2005) model used maximum plant height and phenology to drive plant height elongation; Kotera and Nawata (2007) only considered temperature as driving variable. However, soil water stress was insufficiently considered to crop plant height simulation.

Growth function is generally used to denote an analytical function that connect dry weight to time (Thornley and France, 2007). At present, common growth functions used to study biological ontogeny, and mainly include Gompertz (Gompertz, 1825), Logistic (Verhulst, 1838), Mischerlich (Mitscherlich, 1928), Richards (Richard, 1959), Von Bertalanffy (Von Bertalanffy, 1957), and Weibull (Weibull, 1951). Von Bertalanffy function was proposed by Von Bertalanffy (1957) and later was used to simulate the height of trees (Oyamakin and Chukwu, 2014). Richards function evolved from the Von Bertalanffy function (Richard, 1959), and evolved into three functions such as Logistic, Gompertz, and Mischerlich(Xing et al., 1998; Zwietering et al., 1990). Most of these growth functions were utilized to simulate the development of animals and trees. In recent years, a small number of studies have applied them to the ontogeny of field crops (Setiyono et al., 2008; Wu et al., 2015).

Winter wheat is the main staple food in arid and semi-arid areas of northern China, where drought is the principal limiting factor to wheat production. Studies have shown that severe soil water stress can lead to a reduction in wheat canopy height (Ali et al., 2007; Sun et al., 2014; Xiangxiang et al., 2014). Therefore, understanding and modeling the response of plant height to water stress are of great importance. In this study, modeling of plant height under different levels of soil water stress was investigated.

The objectives of this study were (1) to establish a temperature response function $f(T)$ and a soil water stress response function $f(W)$ to quantify the response of plant height of winter wheat to temperature and soil water stress based on controlled field experiments; (2) to create and evaluate new plant height models of winter wheat that took into account soil water stress through modifications of six common growth functions of Gompertz, Logistic, Mischerlich, Richards, Von Bertalanffy, and Weibul; and (3) to compare the different new wheat plant height models and identify the optimal one for future simulations of plant height of winter wheat in arid and semiarid regions.

2. Materials and methods

2.1. Experiments of soil water stresses at different growth stages of winter wheat

2.1.1. Experiments in plexiglass columns under rainout shelter

The first batch of experiments of soil water stresses at different growth stages of winter wheat were conducted in the Key Laboratory for Agricultural Soil and Water Engineering in Arid Area of Ministry of Education, Northwest A&F University (34°17′N, 108°04′E, 506 m) in China. Wheat crops were planted in plexiglass columns placed under a rainout shelter for two consecutive growing seasons of 2014–2015 and 2015–2016. The data of 2014–2015 was used for developing and parameterizing new simulation models of plant height. The data of 2015–2016 was used to evaluate the established the newly plant height models.

The height, inner and outer diameter of plexiglass columns were 60 cm, 38 cm and 40 cm respectively. There were several small pores and a $1-2$ cm interlayer at the bottom of each column. A column of four small pores ($\varnothing = 2$ cm) were reserved on the side of each column for installations of soil water sensors at 15, 25, 35, and 45 cm from the top edge. The installed soil water sensors (EC-5, Decagon Company, U.S.A) and weighing sensors (MH1124 − 250 kg, MHsensor Company, Germany) measured soil water content and evapotranspiration (ET) at a daily step respectively. A data logger (CR3000, Campbell Company, U.S.A) was used to record data once an hour automatically.

Two early-ripening cultivars ('*Pumai 9*' and '*Xiong 979*'), two middle-ripening cultivars ('*Xiaoyan* 22' and '*Xigao 2*'), and two late-ripening cultivars ('*Xinmai 23*' and '*Zhengmai 7698*') of winter wheat were planted. The columns were refilled with mixed local soil *Luo* soil layer by layer, with a layer depth of 50 cm and a bulk density of 1.2 g cm^{-3}. The field capacity and permanent wilting point of top soil were 0.280 and 0.131 $cm^3\,cm^{-3}$ in the 2014–2015 growing season and 0.291 and 0.142 $cm^3\,cm^{-3}$ in the 2015–2016 growing season, respectively. For fertilizer management, a mixture of 0.347 g urea and 0.2 g KH_2PO_4 per kg dry soil was applied as basal fertilizer. The top surface of each column was split into six equal sectors. Ten wheat seeds of each cultivar were placed in a corresponding sector, which amounted to a planting density of 529 plant m^{-2}. The planting dates were October 21st in 2014 and October 19th in 215. The harvest dates were May 27th in 2015 and June 1st in 2016.

The experimental design included two factors of water-stress period and irrigation depth (Table 1). The water-stress period included four levels, i.e. water stress at winter stage (D1), greening stage (D2), jointing stage (D3), and grain-filling stage (D4). The irrigation depth included two levels of I1 (45 mm) and I2 (90 mm) based on the average water requirements of winter wheat in this region. Additionally, a treatment with 90-mm irrigations at all four different stages (CK) and another treatment without any irrigation at any stage (D) were designed for comparisons. Hence, there were a total of sixty different treatments involved. There were three replicates for each treatment, which led to a total of 30 plexiglass columns. An irrigation of 90 mm was applied to each column two weeks before planting to guarantee the water requirements for emergence and juvenile growth of winter wheat. More details about the experiment could be found in the study by Liu et al. (2016).

2.1.2. Experiments in open field under rainout shelter

The second batch of experiments of soil water stresses at different growth stages of winter wheat were conducted in open fields under a giant rainout shelter in two consecutive growth seasons of 2012–2013 and 2013–2014. The experiment site was same as the previous

Table 1
Irrigation treatments in the soil column experiments of water stresses at different growth stages of winter wheat under rainout shelter, mm.

Treatments	Pre-sowing	Wintering	Greening	Jointing	Grain filling	Total irrigation depth
I1D1	90	0	45	45	45	225
I1D2	90	45	0	45	45	225
I1D3	90	45	45	0	45	225
I1D4	90	45	45	45	0	225
I2D1	90	0	90	90	90	360
I2D2	90	90	0	90	90	360
I2D3	90	90	90	0	90	360
I2D4	90	90	90	90	0	360
CK	90	90	90	90	90	450
D	90	0	0	0	0	90

[a] I1 and I2 represent the irrigation levels of 45 and 90 mm; D1, D2, D3, and D4 represent soil water stresses at the growth stages of wintering, greening, jointing, and grain filling; CK and D represent the control and no-irrigation treatment, respectively.

experiments. The data of these experiments were mainly used to verify the newly developed plant height simulation model of winter wheat under field conditions. For weather conditions, the daily temperatures and solar radiation in 2012–2016 at the experimental site were shown in Fig. 1.

The soil type of the experimental site was also local *Lou* soil, with a pH of 8.14, total organic carbon of 8.20 g kg^{-1}, and total nitrogen of 0.62 g kg^{-1} in the 0 – 20 cm soil layer. The area of each plot was about 8.0 m^2. Adjacent plots were separated by polyethylene plastic films buried 1.5 m below soil surface to prevent subsurface water flow. The winter wheat cultivar tested was '*Xiaoyan 22*', a very popular cultivar planted in the Guanzhong Plain where the experimental site is located. The planting dates were October 15th both in 2012 and 2013. Dry wheat seeds were sown in drill, with a planting depth of 5 – 6 cm, row spacing of 25 cm, and planting density of 400 plant m^{-2}. The harvest dates were June 1 st in 2013 and June 7th in 2014, respectively. The fertilizer application rate was the same for all treatments, with a base fertilizer of 140 kg N ha^{-1} and 50 kg P_2O_5 ha^{-1} but without top dressing.

The experimental factors also included irrigation levels and water-stress periods (Table 2). Based on the average water requirements of winter wheat in this region, two irrigation levels of I'1 (40 mm) and I'2 (80 mm) were involved. However, unlike the plexiglass columns experiments, the whole life cycle of winter wheat was divided into five different development stages in the open field experiments, i.e. wintering, greening, jointing, heading, and grain filling. Soil water stress occurred at a single growth stage might have relatively limited influences, but water stress occurred at two adjacent stages might cause more serious influences on wheat growth. In this case, each water-stress period included two adjacent growth stages, i.e. wintering + greening (D'1), greening + jointing (D'2), jointing + heading (D'3), and heading + grain-filling (D'4). Thus, there was consequently a total of eight treatments, with three replicates for each treatment (Table 2). A total of 24 plots followed a split-plot experimental design and were arranged under a giant movable rainout shelter to exclude the influences of natural precipitation.

A representative quadrat of 1 m^2 was randomly selected and marked in each plot to determine the final yield and plant height, which must not be disturbed during the whole growing season. Regular soil and plant sampling were conducted at a random place covered by crop plants but outside the quadrat. During the experiments, a meter ruler was used to measure the heights of representative winter wheat plants between 11:30 a.m. and 13:30 p.m. in the quadrat. The frequency of plant height measurement was twice a week before jointing and once a week after jointing. More experimental details and results could be found in the research by Yao et al. (2015).

2.2. Development of plant height simulation models of winter wheat

2.2.1. Growth functions

The Richards function (Eq. 4) is evolved from the generalized Von Bertalanffy function (Eq. 5). The other growth functions evolved from the Richards function includes Gompertz (Eq. 1), Logistic (Eq. 2), and Mischerlich (Eq. 3) three functions. Weibull function (Eq. 6) was developed by Weibull (1951)

$$H_G = a_G \times e^{-b_G \exp(-c_G x)} \tag{1}$$

$$H_L = \frac{a_L}{1 + b_L \exp(-c_L x)} \tag{2}$$

$$H_M = a_M \times (1 - b_M \exp(-c_M x)) \tag{3}$$

$$\begin{cases} H_R = a_R \times (1 - b_R \times \exp(-c_R x))^{\frac{1}{1-m}} & m < 1 \\ H_R = a_R \times (1 + b_R \times \exp(-c_R x))^{\frac{1}{1-m}} & m > 1 \end{cases} \tag{4}$$

$$H_V = a_V \times (1 - b_V \times \exp(-c_V x))^3 \tag{5}$$

$$H_W = a_W \times (1 - \exp(-b_W x^{c_W})) \tag{6}$$

Where, H_G, H_L, H_M, H_R, H_V, and H_W are the simulated plant height by the above six growth functions, respectively; x is the thermal time, ℃ day^{-1}; a_G, a_L, a_M, a_R, a_V, and a_W are the maximum potential plant heights corresponding to the six growth functions, cm; b_G, b_L, b_M, b_R, b_V, and b_W are the initial growth parameters, dimensionless; c_G, c_L, c_M, c_R,

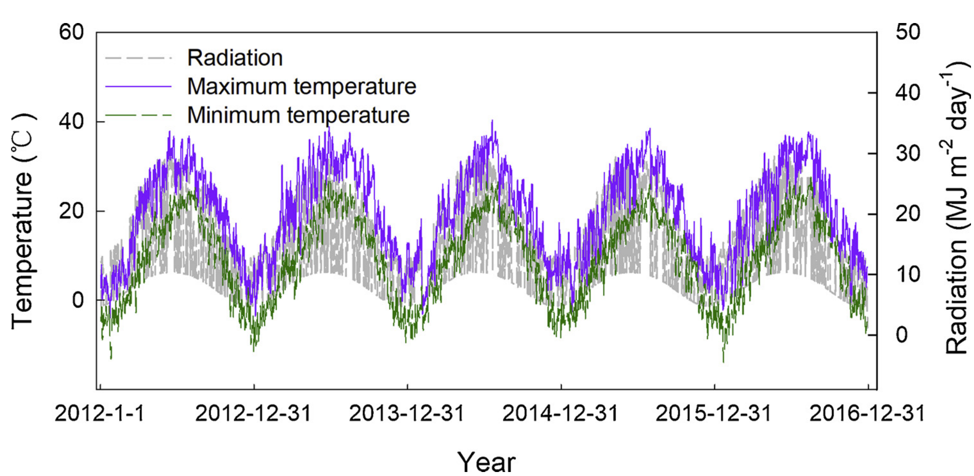


Fig. 1. Daily maximum and minimum temperatures and solar radiations of 2012–2016 at the experimental site at Yangling, Shaanxi province, China.

Table 2
Irrigation treatments in the open field experiments of water stresses at different stages of winter wheat under rainout shelter, mm.

Treatments	Wintering (12–15)[b]	Greening (03–15)	Jointing (04–15)	Heading (05-1)	Grain filling (05–15)	Total irrigation depth
I'1D'1[a]	0	0	40	40	40	120
I'1D'2	40	0	0	40	40	120
I'1D'3	40	40	0	0	40	120
I'1D'4	40	40	40	0	0	120
I'2D'1	0	0	80	80	80	240
I'2D'2	80	0	0	80	80	240
I'2D'3	80	80	0	0	80	240
I'2D'4	80	80	80	0	0	240

[a] I'1and I'2 represent irrigation levels of 40 and 80 mm; D'1, D'2, D'3, and D'4 represent soil water stresses at the stages of wintering + greening, greening + jointing, jointing + heading, and heading + grain filling, respectively.
[b] The actual dates for irrigation are presented in mm-dd format in the parentheses.

c_V, and c_W are the growth rate parameters, dimensionless; and m is the growth velocity parameter, dimensionless.

The plant height H_i of winter wheat on the i-th day (H_i) is the sum of the plant height H_{i-1} of previous day (H_{i-1}) and the plant height elongation on the i-th day (ΔH_i), namely, the plant height on a given day is determined by the existing plant height and the net elongation of plant height on the i-th day.

$$H_i = H_{i-1} + \Delta H_{net,xi}(dx/di) \tag{7}$$

where, H_i and H_{i-1} ***are*** the plant height on the i-th day and on the previous day, cm; $\Delta H_{net,xi}$ ***is the*** elongation rate of plant height with respect to thermal time x on the i-th day, cm x_i^{-1}; and (dx/di) is the change of thermal time on the i-th day, °C day^{-1}.

2.2.2. Models for plant height elongation of winter wheat

Based on the assumption that temperature and soil water content directly affect plant height elongation rate rather than state variables of plant height, the first derivatives of six growth functions (i.e. Gompertz, Logistic, Mischerlich, Richards, Von Bertalanffy, and Weibull), which were modified by temperature response function $f(T)$ (Eq. 14) and soil water stress response function $f(W)$ (Eq. 17), were used to quantify the influences of temperature and soil water stress on plant height elongation (Eqs. 8–13). We denoted these simulation models of winter wheat plant height under water stress as Mod-Geo, Mod-Log, Mod-Mis, Mod-Ric, Mod-Von, and Mod-Wei, respectively. Additionally, it was assumed that winter wheat reached its maximum height at flowering stage in this study.

$$\Delta H_{G,net,xi} = \frac{dH_G}{dx} = \frac{a_G b_G c_G}{e^{(c_G x + b_G \exp(-c_G x))}} f(T) f(W) \tag{8}$$

$$\Delta H_{L,net,xi} = \frac{dH_L}{dx} = \frac{a_L b_L c_L \exp(-c_L x)}{(1 + b_L \exp(-c_L x))^2} f(T) f(W) \tag{9}$$

$$\Delta H_{M,net,xi} = \frac{dH_M}{dx} = a_M b_M c_M \exp(-c_M x) f(T) f(W) \tag{10}$$

$$\Delta H_{R,net,xi} = \frac{dH_R}{dx} = \mp \frac{a_R b_R c_R \exp(-c_R x)}{1-m} (1 \pm b_R \exp(-c_R x))^{\frac{m}{1-m}} f(T) f(W) \tag{11}$$

$$\Delta H_{V,net,xi} = \frac{dH_V}{dx} = 3 a_V b_V c_V (1 - b_V \exp(-c_V x))^2 \exp(-c_V x) f(T) f(W) \tag{12}$$

$$\Delta H_{W,net,xi} = \frac{dH_W}{dx} = a_W b_W c_W x^{c_W - 1} \exp(-b_W x^{c_W}) f(T) f(W) \tag{13}$$

where, $\Delta H_{G,net,xi}$, $\Delta H_{L,net,xi}$, $\Delta H_{M,net,xi}$, $\Delta H_{R,net,xi}$, $\Delta H_{V,net,xi}$, and $\Delta H_{W,net,xi}$ are the first derivatives of Gompertz, Logistic, Mischerlich, Richards, Von Bertalanffy, and Weibull function modified by the temperature response function $f(T)$ and the water stress response function $f(W)$, respectively, which are used to quantify the elongation rate of plant height of winter wheat on the i-th day, cm x_i^{-1}; dH_G, dH_L, dH_M, dH_R, dH_v, and dH_W are the daily elongation rates of plant height of the six corresponding growth functions, cm; and dx is the daily change of thermal day, °C day^{-1}.

The temperature response function $f(T)$ was established based on four cardinal temperatures (i.e. BT, OT1, OT2, and CT) of winter wheat summarized by Soltani et al. (2012), which were set 0, 25, 28 and 40 °C, respectively.

$$f(T) = \begin{cases} 0 & T \le BT \\ (T - BT)/(OT1 - BT) & BT < T < OT1 \\ 1 & OT1 \le T \le OT2 \\ (CT - T)/(CT - OT2) & OT2 < T < CT \\ 0 & T \ge CT \end{cases} \tag{14}$$

where, BT is the base temperature, °C; $OT1$ is the lower optimum temperature, °C; $OT2$ is the upper optimum temperature, °C; CT is the ceiling temperature, °C.

In this study, the relative soil water availability A_w (Eq. 15–16) was used as the index of soil water stress of soil water stress response function (Hanks, 1974; Kang et al., 2000; Liu et al., 2016). Since the root growth was not observed, the average relative soil water availability of 0 − 60 cm soil layer was adopted during the whole growing season in plexiglass columns experiments. For the field experiments under rainout shelter, since soil water contents were only discretely sampled during the whole growing season, the simulated soil water contents by using the DSSAT-CERES-Wheat model were used to calculate A_w instead.

$$A_{w,i} = \frac{\theta_{a,i} - \theta_{wp,i}}{\theta_{f,i} - \theta_{wp,i}} \tag{15}$$

$$A_w = \frac{\sum_{i=1}^{n} A_{w,i}}{n} \tag{16}$$

where, $\theta_{a,i}$ is the actual volumetric soil water content at the i-th soil layer, cm^3 cm^{-3}; $\theta_{f,i}$ is the field capacity at the i-th soil layer, cm^3 cm^{-3}; $\theta_{wp,i}$ is the permanent wilting point in the i-th soil layer, cm^3 cm^{-3}; and $A_{w,i}$ is the relative soil water availability at the i-th soil layer; and n is the number of soil layer.

Consequently, a soil water response function of plant height of winter wheat was established (Eq. 17). In this study, we compared the observed and the simulated plant heights and found that when the values of A_w was greater than 0.65, the plant height elongation rate of winter wheat was not influenced by soil water stress; when the A_w was between 0.3 and 0.65, soil water stress exponentially affected the plant height elongation rate of winter wheat; when A_w was lower than 0.3, soil water stress linearly inhibited the plant height elongation rate of winter wheat until A_w approached 0 where wheat plant height no longer elongated.

Table 3
Estimated parameters for the six different cultivars (two early-ripening cultivars of '*Pumai 9*' and '*Xiong 979*', two middle-ripening cultivars of '*Xigao 2*' and '*Xiaoyan 22*', and two late-ripening cultivars of '*Xinmai 23*' and '*Zhengmai 7698*') in the six new plant height simulation models (Mod-Geo, Mod-Log, Mod-Mis, Mod-Ric, Mod-Von, and Mod-Wei) of winter wheat.

Cultivars	Parameters[a]	Estimated values					
		Mod-Geo	Mod-Log	Mod-Mis	Mod-Ric	Mod-Von	Mod-Wei
Pumai 9	H0	2.0000	2.0000	2.0000	2.0000	2.0000	2.0000
	a	69.0000	69.0000	69.0000	69.0000	69.0000	69.0000
	b	5.7521	24.2993	3.0000	3.0000	1.4923	0.0004
	c	0.0787	0.1206	0.0065	0.0861	0.0626	2.2354
	m	–	–	–	1.3227	–	–
Xinong 979	H0	2.0000	2.0000	2.0000	2.0000	2.0000	2.0000
	a	63.0000	63.0000	63.0000	63.0000	63.0000	63.0000
	b	9.0036	50.1500	3.0000	−2.9999	1.4668	0.0008
	c	0.0948	0.1426	0.0065	0.1051	0.0629	2.7090
	m	–	–	–	1.3227	–	–
Xigao 2	H0	2.0000	2.0000	2.0000	2.0000	2.0000	2.0000
	a	65.0000	65.0000	65.0000	65.0000	65.0000	65.0000
	b	6.7922	40.8489	3.0000	−1.2063	1.5336	0.0002
	c	0.0885	0.1497	0.0073	0.1015	0.0651	2.3962
	m	–	–	–	1.3227	–	–
Xiaoyan 22	H0	2.0000	2.0000	2.0000	2.0000	2.0000	2.0000
	a	83.0000	83.0000	83.0000	83.0000	83.0000	83.0000
	b	6.0210	22.7666	3.0000	3.0000	1.4402	0.0014
	c	0.0746	0.1122	0.0056	0.0861	0.0607	1.8172
	m	–	–	–	1.3227	–	–
Xinmai 23	H0	2.0000	2.0000	2.0000	2.0000	2.0000	2.0000
	a	58.0000	58.0000	58.0000	58.0000	58.0000	58.0000
	b	6.2675	21.8262	3.0000	−1.5255	1.5083	0.0004
	c	0.0835	0.1167	0.0067	0.0913	0.0624	2.2558
	m	–	–	–	1.3227	–	–
Zhengmai 7698	H0	2.0000	2.0000	2.0000	2.0000	2.0000	2.0000
	a	58.0000	58.0000	58.0000	58.0000	58.0000	58.0000
	b	7.1922	34.8120	3.0000	−1.7111	1.5181	0.0002
	c	0.1330	0.1122	0.0067	0.0956	0.0615	2.4559
	m	–	–	–	1.3227	–	–

[a] H0 was plant height at emergence, cm; a was potential maximum plant height, cm; b was Growth initial value parameter; c was rate parameter; and m was hetero velocity growth parameter.

$$f(W) = \begin{cases} 1 & A_w \geq 0.65 \\ \exp(A_w - 0.65) & 0.3 \leq A_w < 0.65 \\ A_w + 0.2 & 0 < A_w < 0.3 \\ 0 & A_w \leq 0 \end{cases} \tag{17}$$

Where, A_w is the relative effective soil water content.

2.2.3. Estimation of model parameters

Experiment of plexiglass columns under rainout shelter in 2014–2015 growing season was used to estimated model parameters. The parameters of the six modified models were estimated based on comparisons between the observed and simulated of plant heights and through the Solver add-in in the MS Excel (Table 3). Since the control (CK) treatment were fully irrigated, its observed plant height at emergence (about 2 cm) was taken as the best estimation of parameter H_0, and its maximum plant height was used as the best estimation of parameter a. The remaining parameters were estimated using the least square method. Finally, a set of parameter values was obtained for each wheat cultivar, which could satisfactorily meet the simulation precision requirements for all treatments (Table 3). Then, the differences between the observed and simulated wheat plant heights were compared

2.3. Model evaluation

Model evaluation was based on experiment of plexiglass columns under rainout shelter in 2015–2016 growing season. The statistic of root mean square error (RMSE; Eq. 18) and Willmott Index of Agreement (WIA; Eq. 19) were used to evaluate the accuracy of the newly established model for plant height simulation through comparisons between model simulations and field observations of plant height.

The point where with the highest growth rate is defined as inflection point of ontogeny curve (Thornley and France, 2007). Therefore, another index of model evaluation was the simulation accuracy of inflection point of plant height.

$$RMSE = \sqrt{\frac{1}{n} \times \sum_{i=1}^{n} (s_i - o_i)^2} \tag{18}$$

$$\text{WIA} = 1 - \frac{\sum_{i=1}^{n} (o_i - s_i)^2}{\sum_{i=1}^{n} (|o_i - \bar{o}| + |s_i - \bar{o}|)^2} \tag{19}$$

where, n is the sample size; s_i is the simulation; o_i is the observation; and $\bar{o}$ is the averaged observation.

3. Results

3.1. Simulating wheat height dynamics in 2014–2015 growing season

According to the results of soil water stress experiment, it was found that wheat height elongation rate was negatively influenced by water stress. The stem elongation rate of treatment D (no irrigation) was close to zero. When water stress occurred at greening and jointing stages (D2 and D3), stem elongation slowed down significantly (Fig. 2c-f).

Each new model was able to satisfactorily simulate the dynamics of winter wheat plant height under different treatments when soil water stress occurred at the greening and jointing stages (D2 and D3). However, all of the six new models failed to catch the inflection point of the plant height elongation (Fig. 2c-f), which was probably the main source of simulation error. Among the six new models, plant height elongation rates of the Mod-Mis and Mod-Von models were higher than

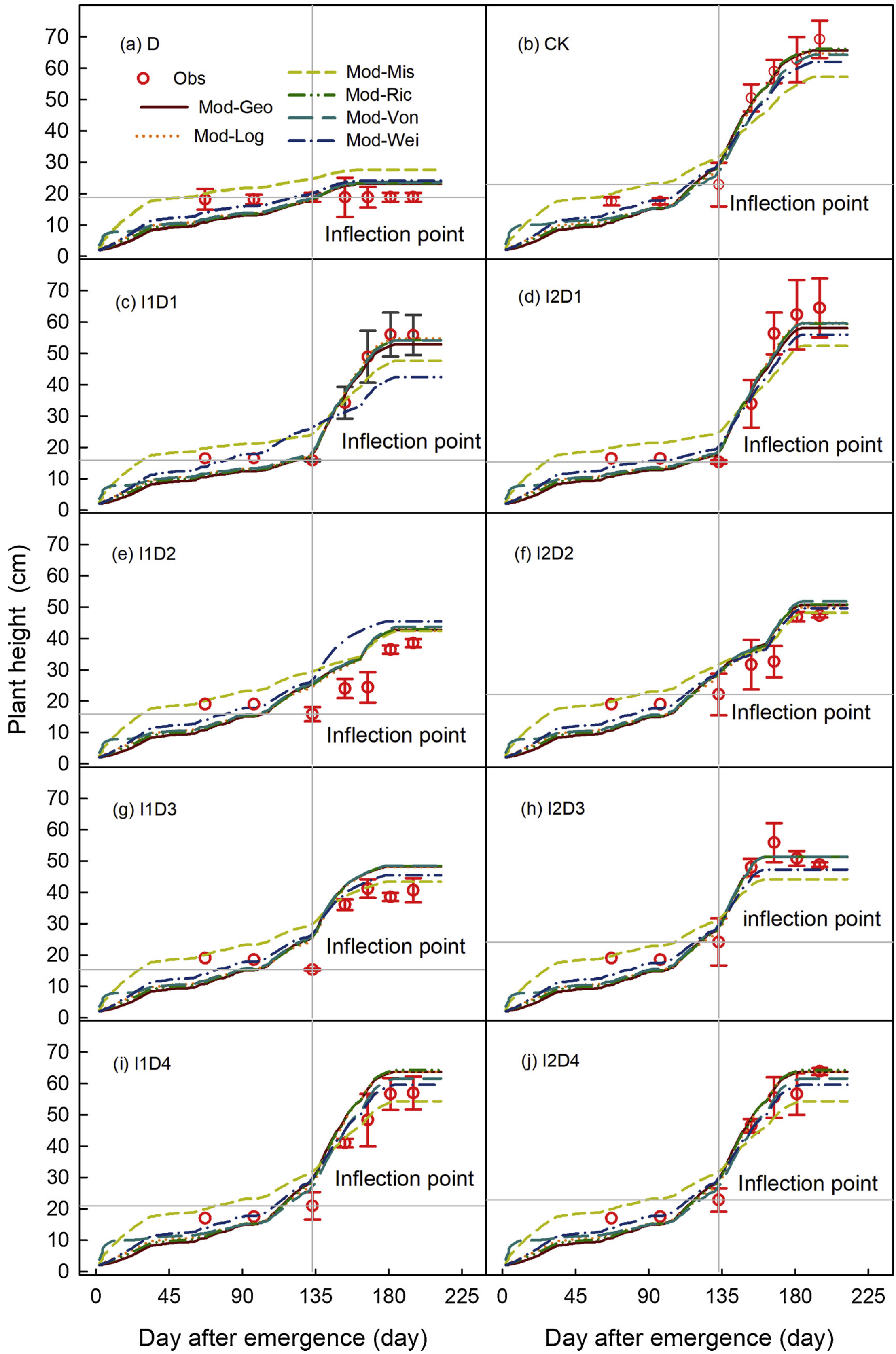
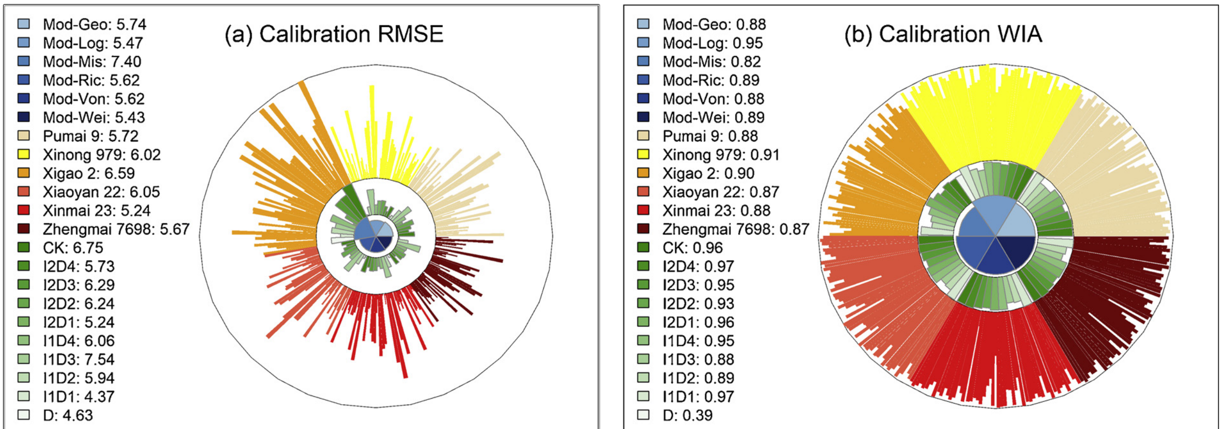


Fig. 2. Dynamics of single plant height of winter wheat in ten different treatments in the 2014–2015 growing season in the soil column experiment under rainout shelter. Symbols D1-D4 represent water stresses at wintering, greening, jointing, and grain-filling stage, while I1 and I2 represent two irrigation depths of 45 and 90 mm, respectively. The error bars are standard deviations of measured winter wheat plant height, cm. The position where the gray vertical line and horizontal line intersected was the inflection point of the observed values.



	CK	I2D4	I2D3	I2D2	I2D1	I1D4	I1D3	I1D2	I1D1	D
MG	6.47	5.55	6.02	6.67	4.99	5.8	7.41	5.93	4.45	4.08
ML	5.69	4.64	5.41	6.26	6.14	5.45	8.1	5.2	3.86	3.96
MM	10.04	8.71	8.66	6.09	4.32	8.12	7.02	7.51	5.97	7.53
MR	5.92	5.21	5.82	6.54	5.31	5.74	7.66	5.69	4.34	4
MV	6.5	5.51	6.08	6	5.25	5.67	7.36	5.82	3.65	4.32
MW	5.89	4.74	5.78	5.91	5.44	5.59	7.68	5.46	3.93	3.9

	CK	I2D4	I2D3	I2D2	I2D1	I1D4	I1D3	I1D2	I1D1	D
MG	0.97	0.98	0.96	0.93	0.96	0.96	0.89	0.89	0.97	0.33
ML	0.98	0.98	0.97	0.93	0.95	0.96	0.87	0.91	0.98	0.91
MM	0.9	0.92	0.88	0.92	0.97	0.89	0.84	0.81	0.94	0.14
MR	0.97	0.98	0.96	0.93	0.96	0.96	0.89	0.9	0.98	0.34
MV	0.97	0.98	0.95	0.94	0.96	0.96	0.88	0.89	0.98	0.29
MW	0.98	0.98	0.96	0.94	0.96	0.96	0.88	0.91	0.98	0.34

Fig. 3. Analysis on the root means square errors (RMSEs) (a) and Willmott Index of Agreement (WIA) (b) of plant height simulations among six different models, six different winter wheat cultivars, and ten treatments in 2014–2015 during model calibration. The outer layer of the pie chart shows the RMSE (a) and WIA (b) between simulated plant height of six different winter wheat cultivars with six different plant height simulation models under 10 treatments in 2014–2015 and six treatments in 2014-205 growing season and corresponding observations (unit: cm and dimensionless). The middle layer of the pie chart shows the RMSE (a) and WIA (b) between simulations and observations that was averaged by six different winter wheat cultivars, which corresponds to the tables in the figures (unit: cm and dimensionless). The inner layer of the pie chart shows the RMSE (a) and WIA (b) between simulations and observations that averaged by six different winter wheat cultivars and then averaged by ten treatments in 2014–2015 growing season, which corresponds to the values in the 1–6 rows of the legend (unit: cm and dimensionless). The values in the 13th to last rows of the legends represent the RMSE (a) and WIA (b) that were averaged by six different models and then averaged by six different cultivars (unit: cm and dimensionless). The abbreviations of MG, ML, MM, MR, MV, and MV in the first column of tables in the figures represent the six different plant height simulation models (i.e. Mod-Geo, Mod-Log, Mod-Mis, Mod-Ric, Mod-Von, and Mod-Wei). The same as below.

those of the other models at the emergence stage, which was not consistent with the physiological characteristics of wheat. In addition, simulated wheat plant heights by the Mod-Mis model were higher than the observations before the inflection point, but lower than observations after the inflection point. The simulated wheat plant heights by the Mod-wei model were close to observations before the inflection point, but lower than observations after the inflection point. However, the plant height dynamic of winter wheat simulated by Mod-Log and Mod-Ric were more consistent with dynamic observations than other models

3.2. Model calibration and validation

According to the RMSE of wheat height simulations for the calibration dataset (Fig. 3a), it was found that the general average RMSE of six different plant height models (i.e. Mod-Geo, Mod-Log, Mod-Mis, Mod-Ric, Mod-Von, Mod-Wei) were 5.74, 5.47, 7.40, 5.62, 5.62, and 5.43 cm (Fig. 3a), and the general average WIA were 0.88, 0.95, 0.82, 0.89, 0.88, 0.89, and 0.89 (Fig. 3b), respectively. Both statistical indicators indicated that Mod-Log and Mod-Wei models obtained the highest simulation accuracy among the six models.

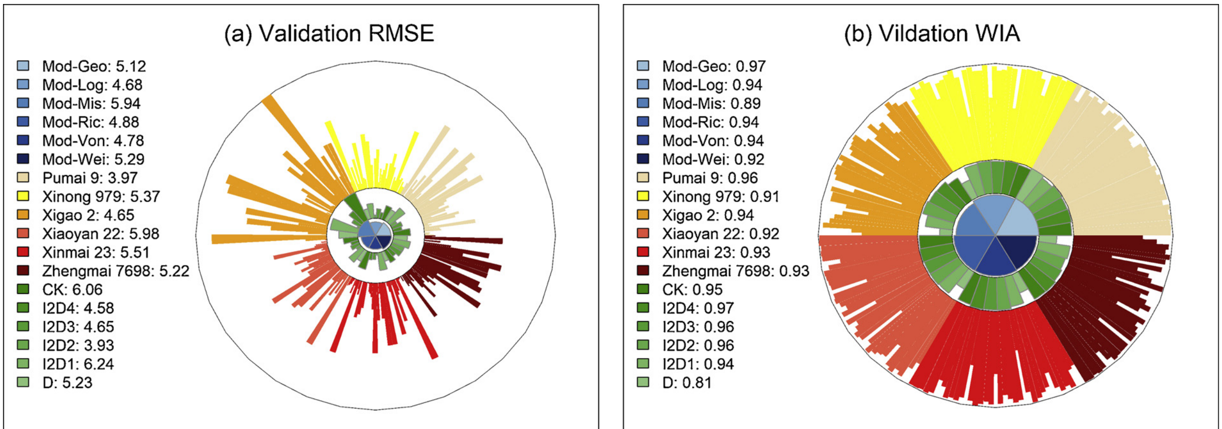
In addition, model performance in wheat plant height simulation varied among different wheat cultivars. The early-ripening cultivar ('*pumai9*' and '*Xinong979*') had higher averaged WIA in plant height simulations in the 2014–2015 (Fig. 3b; with an averaged WIA of 0.90) and 2015–2016 (Fig. 4b; with an averaged WIA of 0.94) growing season, respectively, when compared to middle-ripening and end-ripening cultivars. This was probably due to the different responses of various ripening wheats to soil water stress. However, the differences in plant height simulation accuracy were generally small among different cultivars.

Furthermore, within different irrigation treatments, model simulation accuracies were also different. Both statistical indicators indicated that I1D1, I1D4, I2D1, and I2D4 showed better estimation than I1D2, I1D3, I2D2, and I2D3 by all the six wheat height models (Tables in Fig. 3 a–b). Overall, the plant heights of I2 related treatments were better simulated (with averaged RMSE and WIA of 5.88 cm and 0.95) than I1 related treatments (with averaged RMSE and WIA of 5.98 cm and 0.92) by all of the six models.

Unfortunately, since some of the soil moisture sensors in I1 related treatments were damaged in 2016, only the experimental data of the CK, D, and I2 related treatments (I2D1, I2D2, I2D3, and I2D4) (Table 1) were complete and used for model validation. In model validation, RMSE values indicated that the Mod-Log model obtained the highest simulation accuracy among the six models. However, WIA of the Mod-Geo model was the highest among the six models in wheat height simulation. Generally, based on the results of both calibration and validation with the soil column experiment data, the Mod-Log model was able to obtain higher accuracy than the other simulation models under all of the soil water stress scenarios (Tables in Figs. 3 and 4). The averaged WIA of model calibration and validation were 0.86 and 0.93 (Figs. 3b and 4 b; averaged by CK, I2D4, I2D3, I2D2, I2D1, and D treatments), which means the results of model validation were slightly better than model calibration.

3.3. Model verification with the open field experiment data

Based on the independent data of field experiments conducted under a giant rain shelter in 2012–2013 and 2013–2014, the newly established plant height simulation models of winter wheat were further evaluated. Generally, the Mod-Mis, Mod-Von and Mod-Wei models had bigger simulation errors before the inflection point (Fig. 5), which was the same as model calibration and validation with the soil column experiment data. Moreover, after the inflection point, plant heights simulated by the Mod-Mis model was lower than the observations (Fig.5). However, plant heights simulated by the Mod-Geo, Mod-Log, and Mod-



	Ck	I2D4	I2D3	I2D2	I2D1	D
MG	5.84	4.54	4.8	4.14	6.24	5.18
ML	5.47	4.07	4.61	3.53	5.57	4.82
MM	8.2	5.65	4.53	3.38	7.68	6.2
MR	5.46	4.32	4.57	3.91	5.89	5.1
MV	6.1	4.26	4.13	3.39	6.09	4.73
MW	5.31	4.61	5.25	5.26	5.96	5.35

	Ck	I2D4	I2D3	I2D2	I2D1	D
MG	0.96	0.97	0.96	0.98	0.95	0.98
ML	0.96	0.98	0.96	0.97	0.96	0.79
MM	0.89	0.94	0.94	0.96	0.89	0.71
MR	0.96	0.97	0.96	0.96	0.95	0.8
MV	0.95	0.97	0.97	0.97	0.95	0.81
MW	0.96	0.97	0.95	0.93	0.95	0.77

Fig. 4. Analysis on the root means square errors (RMSEs) (a) and Willmott Index of Agreement (WIA) (b) of plant height simulations among six different models, six different winter wheat cultivars, and six treatments in 2015–2016 growing season during model validation. The outer layer of the pie chart shows the RMSE (a) and WIA (b) between simulated plant height of six different winter wheat cultivars with six different plant height simulation models under six treatments in 2014-205 growing season and corresponding observations (unit: cm and dimensionless). The middle layer of the pie chart shows the RMSE (a) and WIA (b) between simulations and observations that was averaged by six different winter wheat cultivars, which corresponds to the tables in the figures (unit: cm and dimensionless). The inner layer of the pie chart shows the RMSE (a) and WIA (b) between simulations and observations that averaged by six different winter wheat cultivars and then averaged by six treatments in 2015–2016 growing season, which corresponds to the values in the 1–6 rows of the legend (unit: cm and dimensionless). The values in the 13th to last rows of the legends represent the RMSE (a) and WIA (b) that were averaged by six different models and then averaged by six different cultivars (unit: cm and dimensionless). The abbreviations of MG, ML, MM, MR, MV, and MV in the first column of tables in the figures represent the six different plant height simulation models (i.e. Mod-Geo, Mod-Log, Mod-Mis, Mod-Ric, Mod-Von, and Mod-Wei). The same as below.

Ric models were close to the observation when compared with the Mod-Mis, Mod-Von and Mod-Wei models.

The averaged RMSE values of six new models (i.e. Mod-Geo, Mod-Log, Mod-Mis, Mod-Ric, Mod-Von, Mod-Wei) were 7.03, 6.63, 14.41, 6.69, 6.88, and 9.58 cm in 2012–2013 growing season (Fig. 6a), respectively. And, the averaged WIA values of six new models were 0.98, 0.98, 0.88, 0.98, 0.98, and 0.96 in 2012–2013 growing season (Fig. 6c), respectively. Compared with the 2012–2013 model verification results, all of the six new models obtained higher accuracies in the 2013–2014 verification, with averaged RMSE values of 4.64, 4.98, 7.83, 5.12, 4.82, and 4.06 cm (Fig. 6b), and averaged WIA values of six new models were 0.99, 0.99, 0.95, 0.98, 0.99, and 0.99 (Fig. 6d), respectively.

The averaged simulation WIA of irrigation levels I2 and I1 were 0.96, 0.96, 0.96 and 0.97 in 2012–2013 and 2013–2014, respectively (Fig. 6). Contrast to the model calibration and calibration in 2014–2015 and 2015–2016 based on soil column experiment data (Fig. 2), irrigation level had little impact on the accuracies of plant height simulations in the 2012–2013 and 2013–2014 evaluation based on field experiment data. This was probably because $A_w$of $0-100$ cm soil layer in each treatment was greater than 0.65 before the heading period in 2013–2014 (Fig.5) and 2012–2013 growing season. When $A_w$was greater than 0.65, the plant height elongation rate of winter wheat was not affected by soil water content.

In general, the results of double verifications based on the soil column and open field experiments showed that the first derivative of the growth functions of Gompertz, Logistic, and Richards, which were modified by the function of $f(w)$, were able to accurately quantify the dynamic response of plant height elongation rate of winter wheat to soil water stress. Compared with the other models in the four growing seasons of winter wheat, the Mod-Log model had relatively lower error (averaged RMSE and WIA of 5.26 cm and 0.95) in simulating plant height of winter wheat and the accuracy variation was also the smallest (standard deviation of RMSE and WIA of 1.58 cm and 0.05) (Fig. 7).

4. Discussions

Plant height is an important trait in wheat breeding as it is a key parameter affecting lodging and thus grain yield and grain quality (Wurschum et al., 2015). Both genes and environment affect wheat plant height elongation (Kato et al., 1999). In northwest of China, the plant height of winter wheat is at most 20 cm shorter for plants suffering severe water stress than the fully-irrigated ones (Sun et al., 2014). Thus, it is important to understand the influences of soil water stress on plant height of winter wheat. In this study, the first derivative of six common growth functions were modified by a water stress response function $f(w)$and a temperature response function $f(T)$ established in this study to quantify the dynamic response of elongation rate of winter wheat plant height to soil water stress.

The growth function with more flexible inflection point usually had better plasticity, which makes the growth function better fit the biological ontogeny (Paine et al., 2012). The inflection point flexibility depends on the form of the growth function, the number of parameters, and the parameter values (Zeide, 1993). Generally, Logistic, Von Bertalanffy and Richard functions contain three or more than three parameters, while Gompertz and Mischerlich functions contain only one parameter (Tsoularis and Wallace, 2002; Zeide, 1993). What's more, the inflection points of Gompertz and Logistic functions were fixed, while the inflection points of Richards and Von Bertalanffy functions were floating (Tsoularis and Wallace, 2002; Zeide, 1993). Both the numerator and denominator of the first derivative of Logistic and Richards had exponential functions, which lead to more symmetrical curve. Richard (1959) suggested that the plasticity of the Weibull growth function was worse than that of Gompertz, Logistic, and Richards. In general, Mod-Log and Mod-Ric could more reasonably and accurately simulate the plant height of winter wheat (Xing et al., 1998). Winter wheat grows slowly during the wintering stage, and the rapid stem elongation appears in the jointing stage (Milthorpe and Moorby,

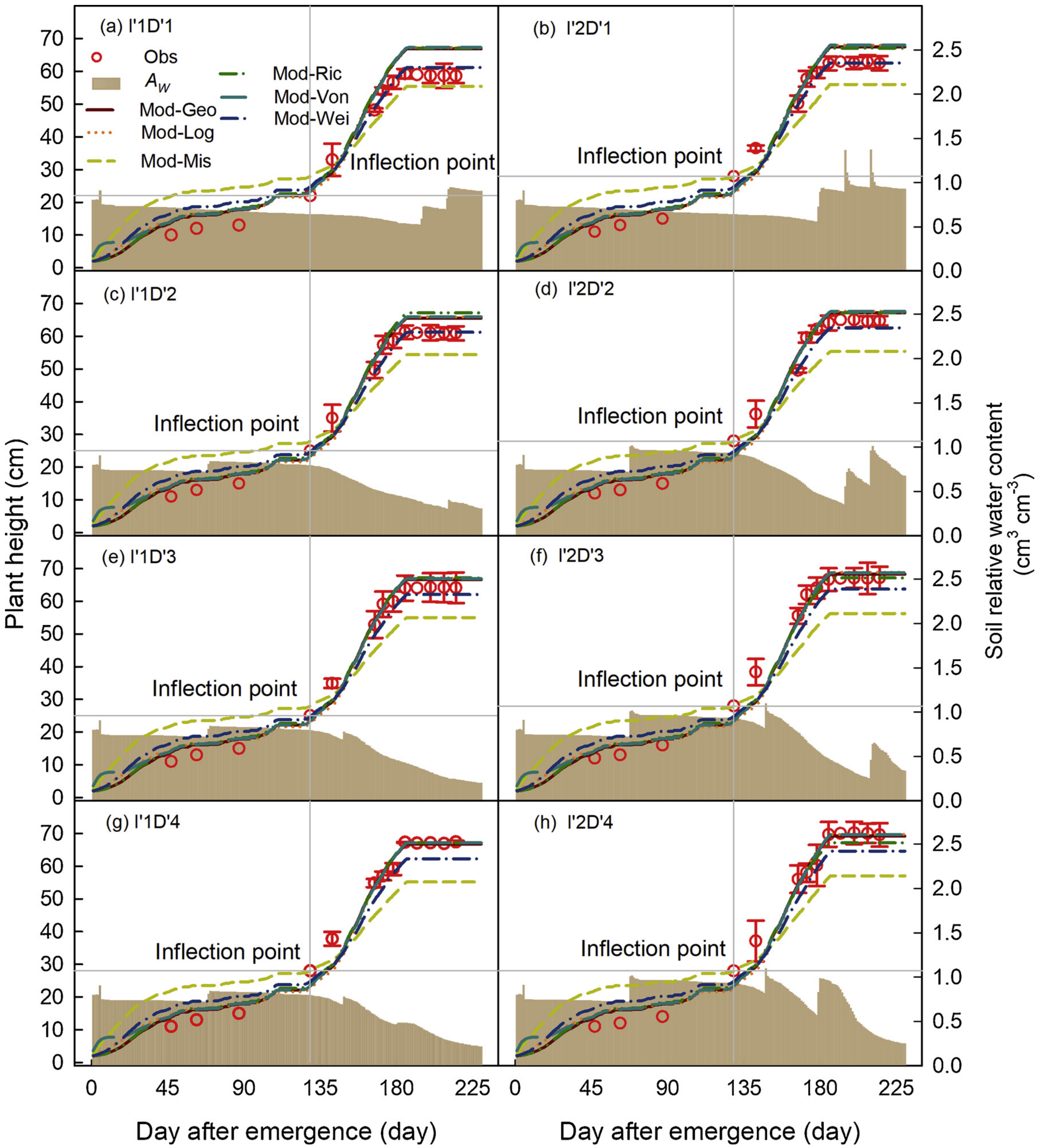
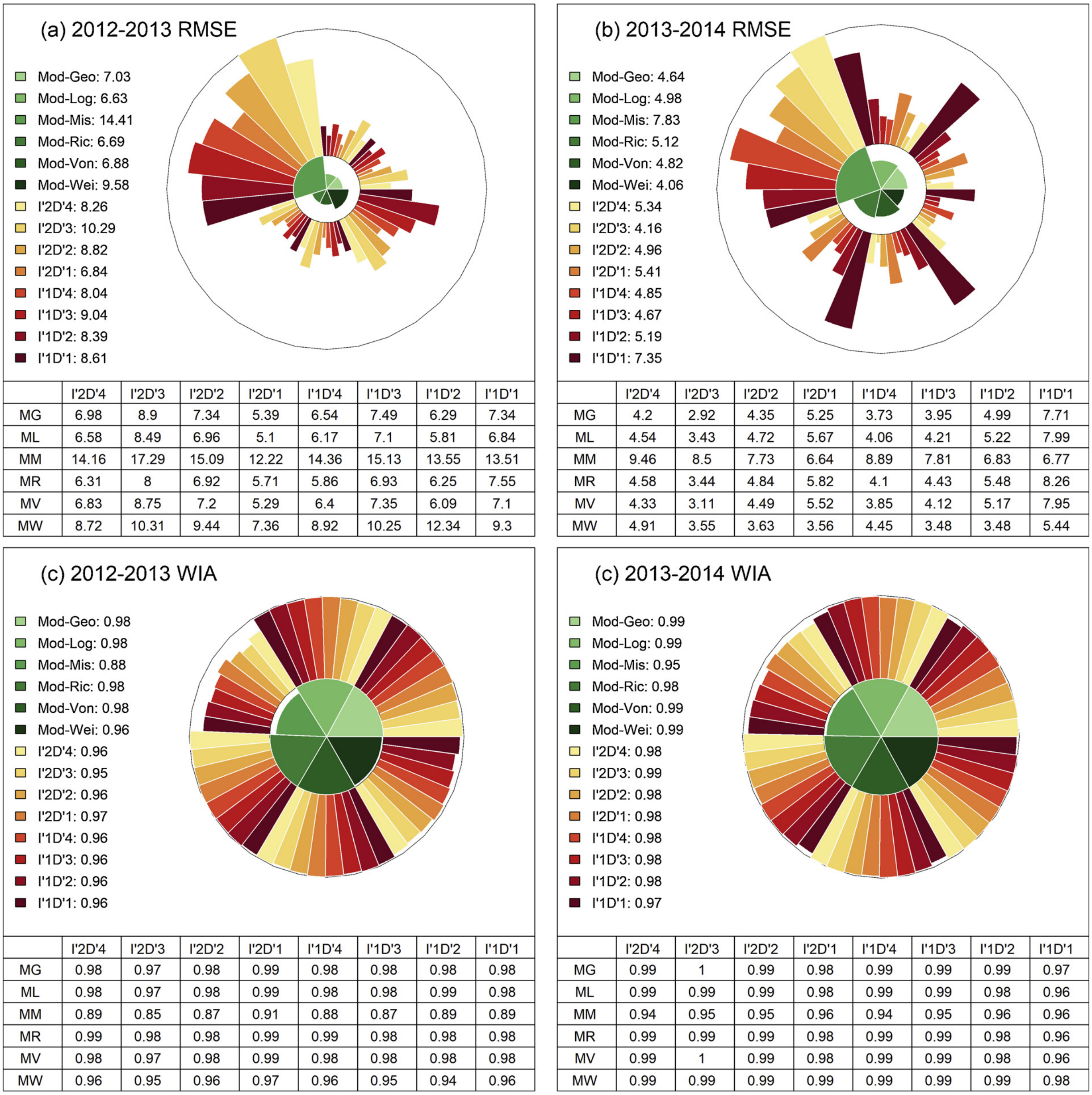


Fig. 5. Dynamics of single plant height of winter wheat in eight different water treatments in the 2013–2014 growing season in the open field experiment under rainout shelter. Symbols D1-D4 represent water stresses at wintering, greening, jointing, and grain-filling stage, while I1 and I2 represent two irrigation levels of 40 and 80 mm, respectively. The error bars are standard deviations of measured winter wheat pant height, cm. The position where the gray vertical and horizontal lines intersected was the inflection point of the observations. The values of relative soil water availability A_w were present as area charts in the figure.

1975). However, the plant height elongation rates simulated by the Mod-Mis and Mod-Von models were rapid after emergence (Figs. 2 and 5), which contradicted the actual growth of winter wheat. Song et al. (2016) suggested that Richards function were more suitable for describing the growth process of organisms. The Richards function has four parameters, but the shape parameter of m may have high uncertainty in parameter estimation (Paine et al., 2012; Xing et al., 1998). Thus, the Mod-Log model obtained the best values of RMSE and WIA among the six different plant height simulation models.

The maximum plant height of representative winter wheat cultivars was 60 − 90 cm in rainfed dryland in Shaanxi Province in the 2010s (Sun et al., 2014). In this study, wheat growth was affected by soil water stress. The range of maximum observed plant height was 20 − 70 cm. Compared with other five models, the Mod-Log model obtained the best general values of RMSE (Fig. 7a; 5.26 cm) and WIA (Fig. 7b; 0.95) between simulated and observed plant height of winter wheat under different water stress scenarios in the four growing seasons. Generally, Logistic function can obtain higher accuracy in height simulation. Weiss et al. (2009) coupled Logistic Function with the CropSyst model to simulate plant height of winter wheat with genetic information in Nebraska. There was a good agreement between the height measurements and simulations

Plant height and leaf area index are two indicators of wheat extensibility growth. In the CERES-Wheat and STICS models. In the CERES-Wheat and STICS models (Brisson et al., 2003), the effects of water stress on wheat extensibility growth were quantified by the ratio of potential root water uptake and potential transpiration (TURFAC, turgor factor). TURFAC equals to 1.0 when there was no water, and



(a) 2012-2013 RMSE

	I'2D'4	I'2D'3	I'2D'2	I'2D'1	I'1D'4	I'1D'3	I'1D'2	I'1D'1
MG	6.98	8.9	7.34	5.39	6.54	7.49	6.29	7.34
ML	6.58	8.49	6.96	5.1	6.17	7.1	5.81	6.84
MM	14.16	17.29	15.09	12.22	14.36	15.13	13.55	13.51
MR	6.31	8	6.92	5.71	5.86	6.93	6.25	7.55
MV	6.83	8.75	7.2	5.29	6.4	7.35	6.09	7.1
MW	8.72	10.31	9.44	7.36	8.92	10.25	12.34	9.3

(b) 2013-2014 RMSE

	I'2D'4	I'2D'3	I'2D'2	I'2D'1	I'1D'4	I'1D'3	I'1D'2	I'1D'1
MG	4.2	2.92	4.35	5.25	3.73	3.95	4.99	7.71
ML	4.54	3.43	4.72	5.67	4.06	4.21	5.22	7.99
MM	9.46	8.5	7.73	6.64	8.89	7.81	6.83	6.77
MR	4.58	3.44	4.84	5.82	4.1	4.43	5.48	8.26
MV	4.33	3.11	4.49	5.52	3.85	4.12	5.17	7.95
MW	4.91	3.55	3.63	3.56	4.45	3.48	3.48	5.44

(c) 2012-2013 WIA

	I'2D'4	I'2D'3	I'2D'2	I'2D'1	I'1D'4	I'1D'3	I'1D'2	I'1D'1
MG	0.98	0.97	0.98	0.99	0.98	0.98	0.98	0.98
ML	0.98	0.97	0.98	0.99	0.98	0.98	0.99	0.98
MM	0.89	0.85	0.87	0.91	0.88	0.87	0.89	0.89
MR	0.99	0.98	0.98	0.99	0.99	0.98	0.98	0.98
MV	0.98	0.97	0.98	0.99	0.98	0.98	0.98	0.98
MW	0.96	0.95	0.96	0.97	0.96	0.95	0.94	0.96

(c) 2013-2014 WIA

	I'2D'4	I'2D'3	I'2D'2	I'2D'1	I'1D'4	I'1D'3	I'1D'2	I'1D'1
MG	0.99	1	0.99	0.98	0.99	0.99	0.99	0.97
ML	0.99	0.99	0.99	0.98	0.99	0.99	0.98	0.96
MM	0.94	0.95	0.95	0.96	0.94	0.95	0.96	0.96
MR	0.99	0.99	0.99	0.98	0.99	0.99	0.98	0.96
MV	0.99	1	0.99	0.98	0.99	0.99	0.98	0.96
MW	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.98

Fig. 6. Analysis on the root mean square errors (RMSEs) and Willmott Index of Agreement (WIA) of plant height simulations by six different models, for six different winter wheat cultivars, and under eight different treatments in 2012–2013 (a, c) and 2013–2014 (b, d) growing seasons during model verification based on the open field experiment data. The outer layer of pie chart shows the RMSE or WIA between simulated plant heights by six different plant height simulation models under eight treatments and corresponding observations, which corresponds to the table in the figures (unit: cm and dimensionless). The inner layer of pie chart shows the RMSE and WIA between simulations and observations that averaged by eight treatments, which corresponds to the values in the 1–6 rows of the legend (unit: cm). The values in the 7th to the last rows of the legend were the RMSE and WIA of plant height simulations and observations that averaged by six different plant height simulation models (unit: cm and dimensionless).

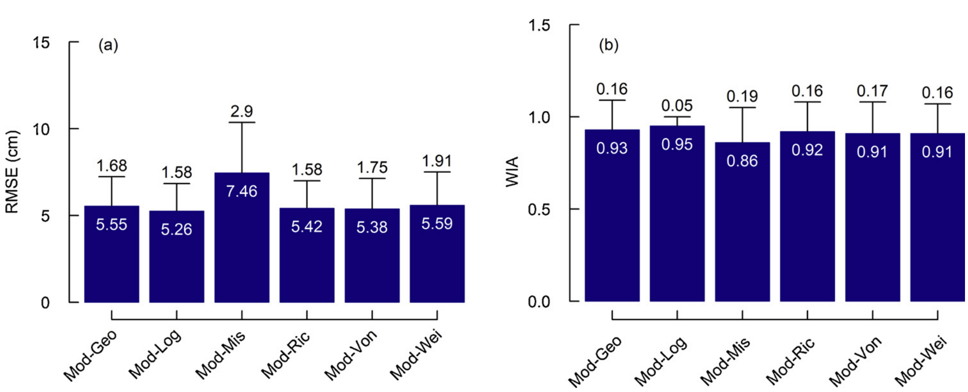


Fig. 7. Averaged root mean square errors (RMSEs) (a) and Willmott Index of Agreement (WIA) (b) of plant height simulations of winter wheat by six different plant height simulation models (Mod-Geo, Mod-Log, Mod-Mis, Mod-Ric, Mod-Von, and Mod-Wei) in the growing seasons of 2012–2013, 2013–2014, 2014–2015, and 2015–2016. The error bars are the standard deviations.

decreases once potential water uptake are less than 1.5 times of potential transpiration, then the extensible growth of wheat will decrease linearly (Guénaëlle et al., 2009; He et al., 2013; Jonesa et al., 2003). In this study, based on the experimental data, it was found that when A_w was greater than 0.65, elongation rate of wheat height was not influenced by soil water content; when A_w was between 0.3 and 0.65, elongation rate of wheat height gradually reduced following an exponential function driven by water stress; when A_w was less than 0.30, elongation rate of wheat height rapidly and linearly reduced driven by water stress until A_w was close to 0 where the elongation stopped. Compared with the results of model calibration and validation with the soil column experiment data, the soil water stress A_w of eight treatments in the open field was greater than 0.65 before the flowering stage and thus the plant height of winter wheat was less affected by soil water stress. Ali et al. (2007) also suggested that the plant height of winter wheat was less affected by lighter soil water stress in open fields.

However, different soil textures have different water-holding capacities (Dexter, 2004). Generally, crops growth in soils with higher water holding capacity are less likely to be influenced by soil water stress and vice versa (Wang et al., 2017). Thus, soil texture may have an influence on the threshold of the water stress response function in this study, which needs further research.

5. Conclusions

In this study, we modified the first derivatives of six different common growth functions (i.e. Gompertz, Logistic, Mischerlich, Richards, Von Bertalanffy, and Weibull) by a soil water stress response function $f(W)$ and a temperature response function $f(T)$ to quantify the influences of soil water stress and temperature on the elongation rate of winter wheat plant height. Consequently, six new plant height simulation models were established. Then, all of six new models were calibrated and evaluated based on data obtained from the soil column and open field experiments conducted under rainout shelter. Some main conclusions were drawn as follows.

(1) The elongation rate of plant height responded linearly and non-linearly to soil water stress. During the linear response stage, the thresholds of relative soil water availability in the water stress response function were 0.0 and 0.30. And, during the non-linear response stage, the thresholds of relative soil water availability were 0.3-0.65. When relative soil water availability was greater than 0.65 or close to 0, elongation rate of wheat plant height was not affected by soil water content or was close to 0.

(2) Compared with the other five models (i.e. Mod-Geo, Mod-Log, Mod-Mis, Mod-Von, and Mod-Wei), the Mod-Log (or modified Logistic) model was able to more accurately simulate the elongation rate and dynamics of winter wheat plant height under different scenarios of soil water stress with less accuracy variation in the 2012–2016 growing seasons. Furthermore, the simulated elongation rate and plant height by the Mod-Log model were more consistent with the actual physiological growth of winter wheat stem.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was supported by the Natural Science Foundation of China (No. 41961124006, 41730645), the Key Research and Development Program of Shaanxi (No. 2019ZDLNY07-03), the “Open Project Fund” from the State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Water and Soil Conservation, Chinese Academy of Sciences and Ministry of Water Resources (No. A314021402-1611), the Science Promotion Project of Test and Demonstration Stations in the Northwest A&F University (TGZX2018-32), and the “111 Project” (No. B12007) of China.

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