PhenoGlad: A model for simulating development in Gladiolus

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ABSTRACT

Crop simulation models are important tools to help farmers in planning management practices and flowering time of cut flowers, like Gladiolus (Gladiolus x grandiflorus Hort.). The objective of this study was to develop a robust Gladiolus phenology model, named PhenoGlad, for field applications. The model describes the timing of developmental stages, including harvest point, the vase life of Gladiolus spikes and the low (chilling) and high (heat) temperature effects on spike quality. The Gladiolus developmental model simulates on a daily basis the cumulative leaf number and the phenology using a non-linear temperature response function and genotype-specific coefficients considering three main phases: corms sprouting phase, vegetative phase, and reproductive phase. Data from nine field experiments conducted during five years (2011–2015) in three locations across the Rio Grande do Sul State and in one location in Santa Catarina State, Brazil, were used. These cultivar x planting dates x years x locations experiments provided a rich data set for parameterizing and evaluating the Gladiolus model. The PhenoGlad model accurately simulated the dynamics of leaf development, final leaf number and the timing of developmental stages among cultivars, planting dates, years and locations, with an overall RMSE of 0.5 leaves for leaf development and final leaf number, 6.5 days for the date of reproductive developmental stages, and 1.3 days for simulating the vase life of harvested spikes. PhenoGlad was also accurate in predicting the effects of chilling and high temperatures damage on florets.

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1. Introduction

Gladiolus (Gladiolus x grandiflorus Hort.) is native of areas in the Mediterranean, and southern and central Africa, propagated by corms, and commercially grown as a cut flower, with a wide range of colours (Schwab et al., 2015). Crop phenology is the result of complex processes of development at different levels, from cell differentiation, organ initiation (morphogenesis) and extends to plant senescence (Hodges, 1991). Both genetic and environmental (biotic and abiotic) factors affect crop phenology (Jones and Kiniry, 1986; Bouman et al., 2004; Setiyono et al., 2007, 2010). The main abiotic factor that drives Gladiolus phenology in the field is air temperature (Shillo and Halevy, 1976a; Streck et al., 2012). Photoperiod may also affect development, but Gladiolus is considered a facultative short-day plant (Shillo and Halevy, 1976b).

Planting date has an important role in regulating growth and quality of field grown Gladiolus, and developmental parameters, like days to germination, sprouting percentage and days to the 6-leaf stage, because they are correlated with air temperature (Adil et al., 2013). Akpinar and Bulut (2011) conducted studies with different Gladiolus species planted in open field in three growing seasons in order to define the most suitable species for flower yield and quality. The authors concluded that climatic factors, such as temperature and light intensity are major factors that drive development and yield of Gladiolus.

Extreme temperatures (low and high) can cause damage to Gladiolus vegetative and reproductive parts (Shillo and Halevy, 1976a). Freezing temperatures during the vegetative phase cause leaf injury whereas during reproductive phase cause severe corolla

damage. Leaves are more tolerant to high temperature (36–40 °C) (Shillo and Halevy, 1976a; International Flower Bulb Centre, 2011) than florets, which can be injured at temperatures above 25 °C (International Flower Bulb Centre, 2011).

Crop simulation models are simple representations of complex processes that drive growth and development during the growing season (Lentz, 1998). In process-based models, processes of the system (plant) are described using mathematical functions, which contain genetic and environmental parameters that affect biological processes (Prusinkiewick, 2004). Therefore, crop simulations models are suitable tools in studies of growth and development of crops in response to the environment (Penning de Vries et al., 1989). Furthermore, crop models provide quantitative information from which management decisions, such as irrigation, fertilization and pest control, can be taken at the field scale (Gary et al., 1998). With regard to temperature effects on crops, there are basically two approaches used in crop models: linear and nonlinear models. Linear models assume a linear relationship between temperature and rate of crop development (Streck et al., 2008). Nonlinear models use a non-linear relationship between temperature and rate of crop development (Landsberg, 1997). This approach was used in the Wang and Engel model for wheat (Wang and Engel, 1998; Streck et al., 2003a,b) to combine genetic and environmental factors and has been applied successfully to several other agricultural crops (Setiyono et al., 2007, 2010; Streck et al., 2007, 2008, 2009, 2011).

Most of crop modeling efforts have been devoted to grain crops, and only a few for ornamental crops (Gary et al., 1998). However, ornamental crop models have a large range of applications, including to assist growers in planning the timing of management practices and to predict flowering time, as growers usually sale their products in markets close to the consumers or for specific holidays and events such as wedding parties and conferences ceremonies. In addition, ornamental crops models should provide information about quality, a major price component of ornamental products (Lentz, 1998).

Models of ornamental species available in the literature include lily (*Lilium longiflorum* Thumb.) (Erwin and Heins, 1990), dahlia (*Dahlia pinnata* Cav.) (Brondum and Heins, 1993), pansy (*Violla* x *wittrockiana* Gams.) (Adams et al., 1997), chrysanthemum (*Dendranthema grandiflora* Tzvelev.) (Larsen and Pearson, 1999), *Campanula carpatica* Jacq. 'Blue Clips', 'Deep Blue Clips' and *Campanula* 'Birch Hybrid' (Niu et al., 2001), miniature rose (*Rosa* L. sp.) (Steininger et al., 2002), 'Freedom' poinsettia (*Euphorbia pulcherrima* Willd) (Liu and Heins, 2002), African violet *(Saintpaulia ionantha* Wendl.) (Streck, 2002), celosia (*Celosia argentea* L.) and impatiens (*Impatiens walleriana* Hook.) (Pramuk and Runkle, 2005), salvia (*Salvia splendens* F.) and marigold (*Tagetes patula* L.) (Moccaldi and Runkle, 2007), 18 bedding plants (Blanchard and Runkle, 2011), and *Brunonia australis* and *Calandrinia* sp. (Cave et al., 2013). The majority of the models developed for the above species were parameterized in greenhouses, not in open air field. No report on a model for Gladiolus was found in the literature.

The objective of this study was to develop a robust Gladiolus phenology model for field applications. In order to have practical application, the model has to predict the timing of developmental stages, including harvest point, the vase life of Gladiolus spikes, and low and high temperature effects on spike quality.

2. Material and methods

2.1. Controlled experiment

A controlled environment experiment was conducted at the Federal University of Pampa (UNIPAMPA), Itaqui, Rio Grande do Sul State (RS), Brazil, part in a growth chamber (PHYTOTRON) and part in a climatic chamber (Model Q315C) with temperature and relative humidity control. Five ambient temperature treatments in continuous dark conditions (7 °C, 16 °C, 25 °C, 30 °C, 35 °C) with 10 replications in a completely randomized experimental design were used. Each replication was a 1.7 l pot filled with soil from the surface layer of a soil classified as Ultisol (USDA, 1999). The ambient relative humidity was 80%.

The cultivar used in this experiment was Amsterdam (white florets). Commercial corms previously vernalized with perimeter between 14 and 16 cm were planted in the pots (one corm per pot) at a 10 cm depth. The pots were filled with the soil and placed in the chamber 24 h before the corms planting. Irrigation with tap water was carried out to maintain the soil close to field capacity.

After planting, each pot was observed daily for plant emergence. Emergence date was defined as the first day when the shoot was visible above the soil. The emergence date of each temperature treatment was defined as the date when 50% of individual plants had emerged. The rate of shoot emergence (day^{-1}) was calculated for each treatment as the inverse of the duration of the sprouting phase (from planting to plant emergence).

2.2. Field experiments

Field experiments were conducted in three locations (Santa Maria, Itaqui and Frederico Westphalen) across the Rio Grande do Sul State and in one location (Curitibanos) in Santa Catarina State, Brazil, located in the southeast of South America (Fig. 1), during five years (2011–2015). Experiments in Santa Maria were irrigated (drip irrigation) whereas experiments in Itaqui, Frederico Westphalen and Curitibanos were rainfed. The experiments in Santa Maria were conducted at the experimental station of the Departamento de Fitotecnia of the Federal University of Santa Maria (UFSM) (latitude: 29° 43′S, longitude: 53° 43′ W and altitude: 95 m), in Itaqui at the experimental station of UNIPAMPA (latitude 29°07′10″ S, longitude 56°32′32″ W and altitude: 50 m), in Frederico Westphalen at the experimental area of UFSM (Frederico Westphalen campus) (latitude: 27° 23′ 47.58″ S, longitude 53° 25′ 41.24″ W and altitude: 489 m), and in Curitibanos at the experimental station of the Federal University of Santa Catarina (UFSC) (latitude: 27° 16′ 24.45″ S, longitude 50° 30′ 10.94″ W and altitude: 992 m). In Santa Maria, an experiment was also conducted in a commercial farm during the Spring 2015, totaling nine field experiments with different cultivars, planting dates, and sites (Table 1).

The four locations (Fig. 1) are different in climate and soil conditions. The average annual temperature in Santa Maria is 19.4 °C, 20.2 °C in Itaqui, 20.4 °C in Frederico Westphalen and 16.5 °C in Curitibanos. The soil in Santa Maria is a transition between a Typic Hapludalf soil and a Rhodic Paleudalf soil, in Itaqui is a Ultisol, in Frederico Westphalen is a Rhodic Hapludox, and in Curitibanos is a Hapludcept (USDA, 1999).

A total of ten cultivars of Gladiolus were used in the experiment (Table 1). The ten Gladiolus cultivars were selected because they are widely grown by commercial farmers and representative of the wide range of colours and developmental cycles of Gladiolus cultivars used in Brazil. A wide range of planting dates was used in the experiments, including two years with monthly planting dates (Table 1). These cultivar x planting dates x years x locations experiments provide a rich data set for parameterizing and evaluating the Gladiolus model.

In all field trials, commercially vernalized corms were planted in beds with two rows, 40 cm among rows and 20 cm among plants within the rows. The planting depth was approximately 10 cm. The experimental design was a complete randomized block design with four replications. Each replication had 10 corms, totaling 40 corms per cultivar. In each experiment, 24 plants of each cultivar were tagged (six plants per replication), and used for measurements.
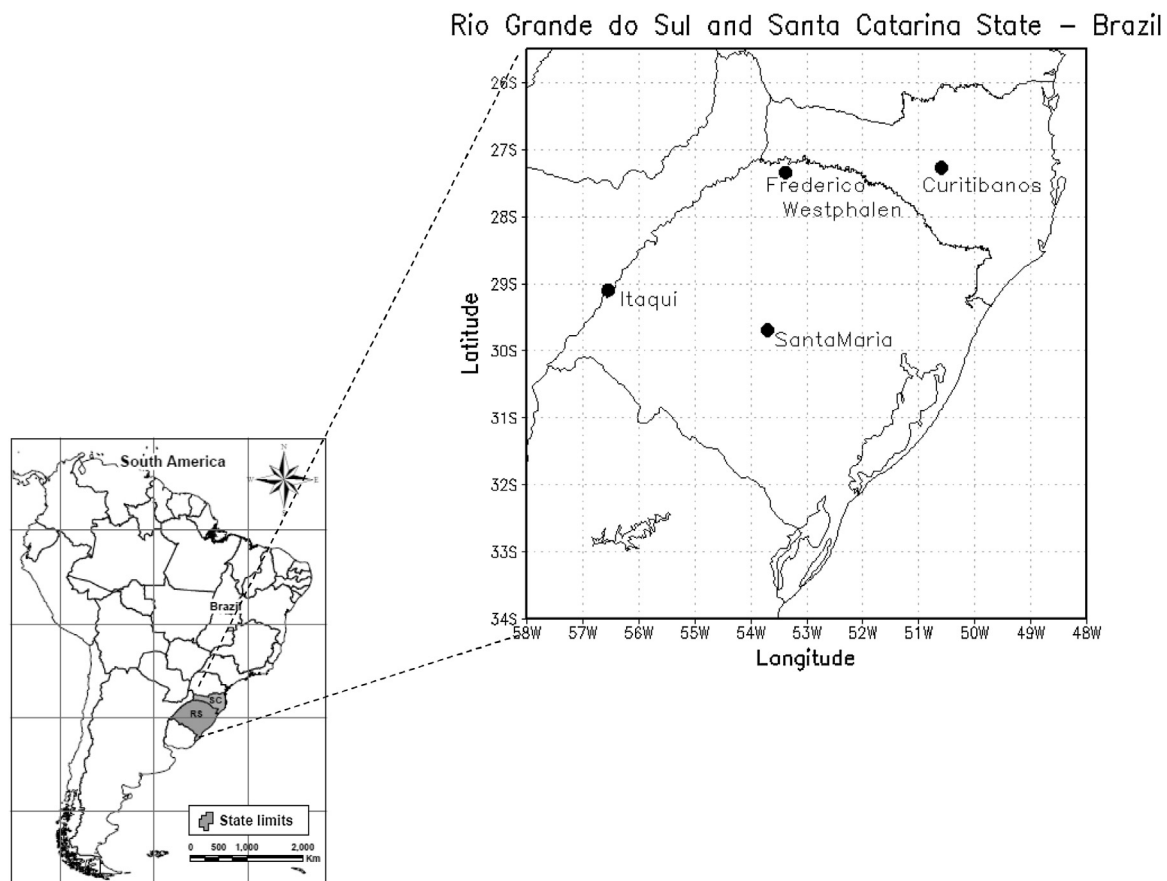
Fig. 1. Maps of South America and Brazil (A), and the States of Rio Grande do Sul and Santa Catarina (B) with the four sites (Santa Maria, Frederico Westphalen, and Curitibanos) where field experiments with Gladiolus were conducted. The field experiment on a commercial farm was in Santa Maria.

Agronomic practices used by local growers were used in the trials, which included fertilization according to chemical soil tests, weed control (by manual hoeing), diseases and insect control (with chemicals), drip irrigation (experiments in Santa Maria) and supporting plants vertically with a plastic net. The on-farm experiment consisted of six 1 m × 22 m beds, one bed with each cultivar (220 plants per cultivar), next to a Gladiolus plantation which had about 5000 plants. Management practices in the on-farm experiment were the same as the farmer did in the commercial plantation. No irrigation was used in the on-farm experiment.

2.3. Plant and weather data collection in the field experiments

During all field experiments, the date of occurrence of the vegetative (V-stages) and reproductive (R-stages) developmental stages were observed on the tagged plants (6 plants per plot) according to phenological scale of Gladiolus (Schwab et al., 2015). The date of emergence (shoots were first visible above the soil) and other developmental stages was considered when 50% of plants have reached them. The cumulative leaf number (CLN) was counted twice a week until the final leaf (flag leaf) was visible (VF). When the spike was first visible at the whorl, plants were observed daily and the following developmental stages were recorded (Schwab et al., 2015): R1.0 = heading, R2 = blooming, R3 = onset of anthesis, R3.4 = half of anthesis, R3.5 = beginning floret senescence, R3.6 = half of florets senesced, R4 = anthesis completed and R5 = end of floret senescence.

Daily weather data were obtained from a conventional weather station of the Brazilian National Weather Service (INMET) located approximately 100 m from the trials in Santa Maria and from an automated weather station located at about 200 m from the trials in Itaqui, about 50 m from the trials in Frederico Westphalen and about 10 km from the trials in Curitibanos. In the on-farm experiment, data were from an automated weather station located 20 m from the trial.

2.4. Postharvest experiment

A vase experiment was conducted in October and November 2015 inside a room with ambient temperature and natural light. The objective of this experiment was to test the model in simulating the progress of reproductive development during vase life of Gladiolus spikes. Ten floral stems (spikes commercially sold) of six Gladiolus cultivars (Purple Flora, Amsterdam, Green Star, White Goddess, Jester and Gold Field) were placed in a 10 l bucket filled with tap water (one bucket per cultivar).

The floral stems were harvested from plants grown in the field (planting was on 28 July 2015) at the R2 stage. Each spike was tagged and developmental stages (R3, R3.4, R3.5, R4 and R5) were observed daily. Minimum and maximum daily air temperature inside the room was measured throughout the experimental period.

2.5. Model description

The Gladiolus development model, named PhenoGlad, simulates Gladiolus phenology on a daily basis. The developmental cycle of Gladiolus is divided into three main phases based on the developmental scale by Schwab et al. (2015): corms sprouting phase, from planting (PL) until emergence (VE) (Fig. 2a), vegetative phase,

Table 1
Experiments in Brazil with locations, Gladiolus cultivars and planting dates (dd/mm/yyyy) used as data sets in the study.

Experiment number	Location	Cultivars	Planting dates
1	Santa Maria	T704 (only on 05/08/2011), Rose Friendship, Peter Pears, Jester	05/08/2011, 02/09/2011, 03/10/2011, 01/11/2011, 01/12/2011, 04/01/2012, 01/02/2012, 07/03/2012, 02/04/2012, 02/05/2012, 01/06/2012, 02/07/2012
2	Santa Maria	Rose Friendship, Amsterdam, Jester	02/08/2012, 03/09/2012, 04/10/2012, 01/11/2012, 03/12/2012, 04/01/2013, 01/02/2013, 01/03/2013, 01/04/2013, 01/05/2013, 03/06/2013, 02/07/2013
3	Santa Maria	T704, Amsterdam, Peter Pears, Green Star, Jester	26/07/2013, 09/09/2013, 31/10/2013
4	Santa Maria	White Friendship, Purple Flora, Rose Friendship (not on 06/03/2014), Amsterdam, Peter Pears (only on 06/03/2014), Green Star, Jester	06/03/2014, 16/04/2014, 26/05/2014
5	Santa Maria	White Friendship, Purple Flora, Rose Friendship, Green Star, Jester, Gold Field	31/07/2014, 23/09/2014, 27/10/2014
6	Itaqui	White Friendship, Purple Flora, Rose Friendship, Green Star, Jester, Gold Field	28/07/2014, 22/09/2014, 26/10/2014
7	Frederico Westphalen	White Friendship, Purple Flora, Rose Friendship, Green Star, Jester, Gold Field	05/08/2014, 29/08/2014, 23/10/2014
8	Curitibanos	Purple Flora, Amsterdam, White Goddess, Green Star, Jester, Gold Field	29/09/2015, 30/10/2015
9	On Farm, Santa Maria	Purple Flora, Amsterdam, White Goddess, Green Star, Jester, Gold Field	27/07/2015

from VE until heading (R1.0) (Fig. 2c) and reproductive phase, from R1.0 until the end of florets senescence (R5). During the vegetative phase, leaf appearance starts at VE and stops when the crop reaches R1 (Fig. 2b).

2.6. Leaf appearance and final leaf number

Leaf development has two parts in the PhenoGlad model (Fig. 2b): Part (i) calculates the cumulative leaf number (CLN), and Part (ii) calculates the final leaf number (FLN). Daily leaf appearance rate (LAR) is calculated using the approach described in Wang and Engel (1998):

$$LAR = LAR_{max}. f(T) \tag{1}$$

where LAR is the daily leaf appearance rate (leaves day^{-1}), LAR$_{max}$ is the cultivar specific maximum daily leaf appearance rate (leaves day^{-1}), and f(T) is the temperature response function (0–1). The f(T) is a version of the beta function:

$$f(T) = [2(T - Tb)^{\alpha} (Topt - Tb)^{\alpha} - (T - Tb)^{2\alpha}]/(Topt-Tb)^{2\alpha} \text{ if } Tb \leq T \leq TB$$

$$f(T) = 0 \text{ if } T < Tb \text{ or } T > TB \tag{2}$$

$$\alpha = \ln2/\ln[(TB-Tb)/(Topt-Tb)] \tag{3}$$

where Tb, Topt and TB are the cardinal temperatures (minimum, optimum and maximum) for LAR, respectively, and T is the average daily air temperature, calculated from the mean of minimum and maximum air temperatures. The cardinal temperatures for LAR were Tb = 2 °C (Shillo and Halevy, 1976a; Hertogh, 1996), Topt = 27 °C (International Flower Bulb Centre, 2011), and TB = 45 °C (Shillo and Halevy, 1976a; International Flower Bulb Centre, 2011). The curve generated by Eqs. (2) and (3) with the cardinal temperatures for LAR is shown in Fig. 3 (green curve). The CLN is calculated

starting at VE by accumulating daily LAR values, i.e., CLN = ∑LAR, until the onset of reproduction.

The FLN is defined at the day of the R1 stage. During the field experiments, we noted that 2–3 days before R1 the LAR is much higher than the LAR during the previous period from VE, probably because the 2–3 uppermost leaves are the smallest and because at this time the floral stem starts its exponential growth in length. In some cultivars this is more pronounced than in others. Eq. (1) does not account for this increase in LAR of the uppermost leaves, but it is important for defining FLN. To account for this increase in LAR of the uppermost leaves on FLN, we introduced an empirical genetic-dependent correction factor (CF), which is added to the CLN at the day of R1:

$$FLN = CLN_{R1.0} + CF \tag{4}$$

where FLN is the final leaf number, CLN$_{R1.0}$ is the CLN calculated at the day of R1 and CF is a correction factor for higher leaf appearance rate of the uppermost leaves, specific for each cultivar.

2.7. Phenological phases

Starting at planting, the developmental stage (DVS) is calculated by accumulating the daily developmental rate (r) values, i.e, DVS = ∑r. DVS is −1 at PL, 0 at VE, 0.8 at R1.0, 1.0 at R2, 1.13 at R3, 1.32 at R3.4 and R3.5, 1.56 at R3.6, 1.84 at R4 and 2 at R5 (Fig. 2e). The choice of these DVS values for each developmental stage was based on previous models of wheat (Streck et al., 2003a) and rice (Streck et al., 2011), where phases and sub-phases where defined in ranges of DVS within −1 (planting) and 2 (crop maturity). The daily developmental rate (day^{-1}) was calculated with the approach by Wang and Engel (1998):
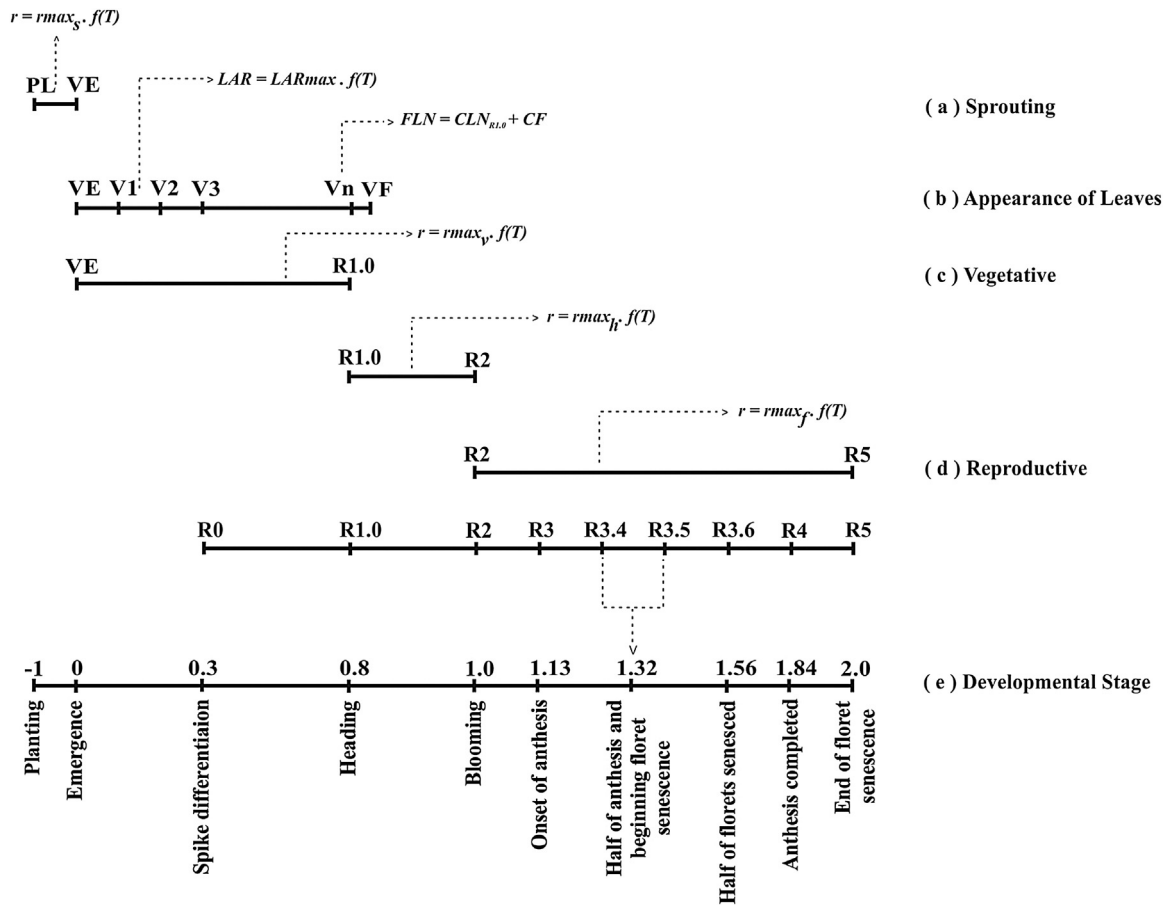
$$r = rmax. f(T) \tag{5}$$

Fig. 2. Schematic timeline and developmental sequence of Gladiolus simulated in the PhenoGlad model. Developmental cycle is divided into main phases (a, c, d) and sub-phases (sub-division within each main phase). The sequence of vegetative stages (V1, V2, V3,...,Vn) in (b) comprises the appearance of leaves during the vegetative main phase. Equations used in simulating each of the main phases and sub-phases are shown. Coding number of each developmental stage are shown in (e). LAR = leaf appearance rate (leaves day^{-1}), LAR$_{max}$ = maximum leaf appearance rate (leaves day^{-1}), f(T) = temperature function, FLN = final leaf number, CLN$_{R1.0}$ = CLN at the day of R1, CF = correction factor for higher leaf appearance rate of the uppermost leaves, VF = flag leaf, r = developmental rate (day^{-1}), rmax$_s$ = maximum developmental rate (day^{-1}) during the sprouting main phase, rmax$_v$ = maximum development rate (day^{-1}) during the vegetative main phase, rmax$_h$ = maximum developmental rate (day^{-1}) during the heading sub-phase, rmax$_f$ = maximum developmental rate (day^{-1}) during the flowering sub-phase. Dashed arrow in (d) indicates that the R-Stages R3.4 and R3.5 occur simultaneously.
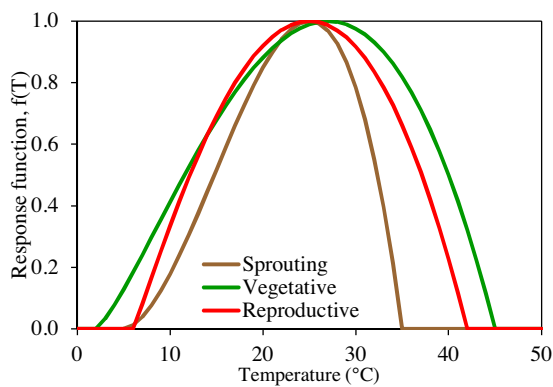

Fig. 3. Temperature response functions f(T) used in the PhenoGlad model to simulate the developmental phases of Gladiolus: sprouting phase (Tb = 5 °C, Topt = 25 °C and TB = 35 °C), vegetative phase (Tb = 2 °C, Topt = 27 °C and TB = 45 °C), and reproductive phase (Tb = 6 °C, Topt = 25 °C and TB = 42 °C).

where r is the daily developmental rate (day^{-1}), rmax is the maximum daily development rate (day^{-1}) at optimum temperature and f(T) is the temperature response function for plant development. The rmax is genotype dependent and varies according to the developmental phase and sub-phase (Fig. 2a, c and d): rmax$_s$ = maximum

developmental rate (day^{-1}) during the sprouting main phase, rmax$_v$ = maximum development rate (day^{-1}) during the vegetative main phase, rmax$_h$ = maximum developmental rate (day^{-1}) during the heading sub-phase, rmax$_f$ = maximum developmental rate (day^{-1}) during the flowering sub-phase.

The temperature response function f(T) in Eq. (5) is the same as in Eqs. (2) and (3), using the average daily air temperature, calculated from the average of minimum and maximum air temperatures, but the cardinal temperatures are different for each developmental phase. In the sprouting phase, the cardinal temperatures are: Tb = 5 °C (Shillo and Simchon, 1973), Topt = 25 °C (from our controlled experiment), and TB = 35 °C (from our controlled experiment). In the vegetative phase, cardinal temperatures are: Tb = 2 °C (Shillo and Halevy, 1976a; Hertogh, 1996), Topt = 27 °C (International Flower Bulb Centre, 2011), and TB = 45 °C (Shillo and Halevy, 1976a; International Flower Bulb Centre, 2011) and in the reproductive phase (heading and flowering sub-phases), cardinal temperatures are: Tb = 6 °C (Hertogh, 1996; Burg, 2004), Topt = 25 °C (International Flower Bulb Centre, 2011), and TB = 42 °C (Shillo and Halevy, 1976a; International Flower Bulb Centre, 2011). The shape of f(T) for each developmental phase is in Fig. 3.

Table 2

Planting dates (dd/mm/yyyy) and experiments with Gladiolus cultivars used for parameterizing the PhenoGlad model. The planting dates were the same for parameterizing the leaf development and the phenology phases unless otherwise stated. LARmax = daily leaf appearance rate, CF = correction factor for defining final leaf number.

Cultivar	Planting dates for parameterization	Experiment number
. . . . Leaf development (LAR$_{max}$ and CF) and phenology		
White Friendship	06/03/2014, 16/04/2014, 31/07/2014, 23/09/2014	4 and 5
Purple Flora	06/03/2014, 26/05/2014, 31/07/2014, 23/09/2014	4 and 5
Rose Friendship	02/09/2011, 03/10/2011, 07/03/2012, 02/05/2012[a]	1
	03/09/2012, 01/03/2013, 01/05/2013, 02/07/2013[b]	2
Amsterdam	03/06/2013, 26/07/2013, 09/09/2013, 31/10/2013	2 and 3
T704	09/09/2013	3
Peter Pears	05/08/2011, 26/07/2013, 09/09/2013, 31/10/2013	1 and 3
Green Star	16/04/2014, 26/05/2014, 31/07/2014, 23/09/2014	4 and 5
Jester	03/09/2012, 01/03/2013, 01/05/2013, 02/07/2013	2
White Goddess	28/07/2015[a]	
	10/11/2014[b]	
Gold Field	31/07/2014, 23/09/2014, 27/10/2014	5
. . . . Chilling		
Jester	02/04/2012	1
. . . . Heat injury		
Jester	31/10/2013	3

[a] Planting dates used for parameterizing the leaf appearance phase.

[b] Planting dates used for parameterizing the phenology model.

2.8. Chilling and heat injury

Injuries due to low and high temperature on Gladiolus are considered in PhenoGlad as follows: if the minimum temperature is lower than −2 °C during at least three days in a row, from DVS = 0 (VE) to DVS = 2.0 (R5) then the crop is killed by frost. If the minimum temperature is lower than or equal to −2 °C during one day or if −2 °C ≤ Tmin ≤ 3 °C during 3 days in a row from DVS ≥ 0.64, then the spike is killed by frost but leaves are only injured slightly (patchy whitening and burning). The DVS value of 0.64 was based on field observations that plants were damaged by chilling temperatures in the experiment used to parameterize the model (Table 2). Heat injury in PhenoGlad is considered when the maximum temperature is greater than or equal to 34 °C during three consecutive days during the reproductive phase (from R1 to R5). These thresholds were selected based on our field experiments as described in the model parameterization section (section 2.9).

The model warns the user about a severe burning of petals and sepals if the simulation ends at R2 (harvest point). If the simulation ends at R5 (end of flowering), the warning is about severe burning and risk that the 3 or 4 uppermost florets on the spike do not open. If the maximum temperature is higher than 48 °C from DVS = 0 to DVS = 2, the upper lethal temperature is reached (Shillo and Halevy, 1976a) and the crop is killed by heat.

2.9. Model parameterization

The PhenoGlad model (leaf appearance and phenology) was parameterized for the ten Gladiolus cultivars with part of the field experiments conducted in Santa Maria (Table 2). The dataset for model parameterization was selected to have a wide range of durations of developmental phases. The temperature response function, f(T) (Eqs. (2) and (3)), for the sprouting phase was parameterized considering Tb = 5 °C (corms storage temperature), Topt = 25 °C and TB = 35 °C from the controlled experiments. The cardinal temperatures for the other developmental phases and for the leaf appearance rate were defined based on the literature and described
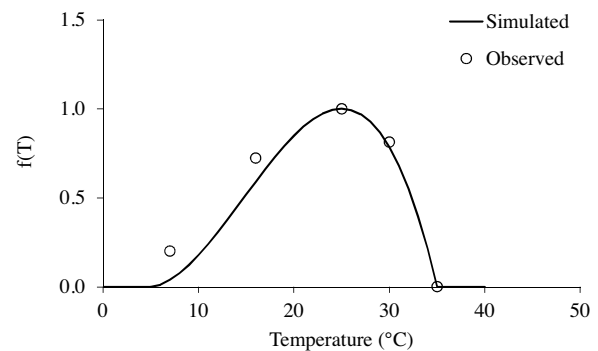

Fig. 4. Temperature response function f(T) used in the PhenoGlad model for the sprouting developmental phase. The circles are the observed values for cultivar Amsterdam in a controlled environment experiment.

in sections 2.6 and 2.7. The warnings of chilling and heat injury were parameterized with two planting dates of cultivar Jester (Table 2). In these two planting dates, low temperature caused killing of spikes (02 April 2012 planting date) and high temperature caused burning of sepals and petals (31 October 2013 planting date), respectively.

The warning of chilling injuries was parameterized according to observations performed in a field experiment, where the Gladiolus spikes were exposed to lethal temperatures (−2 °C) in the 02 April 2012 planting date (Table 2). The warning of heat injury was parameterized according to observations performed in a field experiment, where the Gladiolus spikes were exposed to high temperatures (three consecutive days with maximum temperature higher or equal than 34 °C) during the 31 October 2013 planting date (Table 2). The injury observed in the field was a severe burning on Gladiolus sepals, which caused the failure of the 3 or 4 uppermost florets opening, making Gladiolus spikes unmarketable.

The coefficient LAR$_{max}$ for each cultivar was parameterized by increasing an initial value (0.02 leaves day^{-1}) until obtaining the best fit between observed and estimated CLN values by minimiz-

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Table 3
Summary of meteorological variables (daily minimum, maximum and mean temperature, daily mean solar radiation and accumulated precipitation) during the nine experiments with Gladiolus.

Location	Experiment number	Season	Temperature (°C)			Rad. (MJ m^{-2} day^{-1})	Prec. (mm)
			Min.	Mean	Max.		
Santa Maria	1	Spring/2011	7.6	21.6	39.0	22.1	255.6
		Summer/2011–2012	13.2	26.2	39.0	21.7	364.8
		Autumn/2012	−2.0	17.6	35.6	12.7	349.7
		Winter/2012	−0.4	17.3	33.6	10.8	404.7
		Mean	4.6	20.7	36.8	16.8	$\sum$ = 1374.8
Santa Maria	2	Spring/2012	3.6	22.6	38.2	20.0	588.6
		Summer/2012–2013	10.2	23.8	39.2	20.4	539.0
		Autumn/2013	1.2	17.8	32.6	11.9	350.4
		Winter/2013	0.4	15.2	35.2	11.2	351.8
		Mean	3.8	19.9	36.3	15.9	$\sum$ = 1829.8
Santa Maria	3	Spring/2013	6.0	21.6	35.0	20.6	549.0
		Summer/2013–2014	13.6	26.0	40.2	20.5	454.2
		Mean	9.8	23.8	37.6	20.6	$\sum$ = 1003.2
Santa Maria	4	Autumn/2014	−0.2	17.9	34.2	11.1	454.2
		Winter/2014	−0.2	16.8	33.2	10.3	776.4
		Mean	−0.2	17.4	33.7	10.7	$\sum$ = 1230.6
Santa Maria	5	Spring/2014	10.6	22.8	37.8	19.2	651.0
		Summer/2014–2015	13.0	25.4	37.0	20.3	428.2
		Mean	11.8	24.1	37.4	19.8	$\sum$ = 1079.2
Itaqui	6	Winter/2014	4.0	17.2	32.2	12.6	276.0
		Spring/2014	11.8	24.1	37.5	19.4	384.6
		Summer/2014–2015	14.9	26.5	37.3	19.6	363.6
		Mean	10.2	22.6	35.7	17.2	$\sum$ = 1024.2
Frederico Westphalen	7	Winter/2014	1.1	18.3	32.6	13.9	330.4
		Spring/2014	9.3	22.5	35.8	23.2	659.8
		Summer/2014–2015	14.9	24.5	33.4	23.4	315.0
		Mean	5.2	19.9	34.2	20.2	$\sum$ = 1305.2
Curitibanos	8	Spring/2015	7.7	18.8	31.5	16.2	837.6
		Summer/2015–2016	14.2	22.7	31.2	20.5	132.6
		Mean	11.0	20.8	31.4	18.4	$\sum$ = 970.2
On Farm	9	Spring/2015	0.8	19.4	35.8	13.7	850.6

Table 4
Coefficients of the PhenoGlad model (LAR$_{max}$, CF, rmax$_s$, rmax$_v$, rmax$_h$, rmax$_f$) for the leaf appearance phase and the developmental phases planting to emergence (PL – VE), emergence to heading (VE – R1), and sub phases heading to blooming (R1 – R2), and blooming to end of floret senescence (R2 − R5) for ten Gladiolus cultivars. LARmax = maximum leaf appearance rate (leaves day^{-1}), CF = correction factor in the calculation of final leaf number (unitless), rmax$_s$ = maximum development rate during the PL-VE phase (day^{-1}), rmax$_v$ = maximum development rate during the VE-R1 phase (day^{-1}), rmax$_h$ = maximum development rate during the R1-R2 sub-phase (day^{-1}), rmax$_f$ = maximum development rate during the R2-R5 sub-phase (day^{-1}).

Cultivar	LAR$_{max}$	CF	rmax$_s$	rmax$_v$	rmax$_h$	rmax$_f$
White Friendship	0.1853	0.59	0.0857	0.0190	0.0225	0.0628
Purple Flora	0.1597	1.01	0.0892	0.0187	0.0225	0.0708
Rose Friendship	0.1913	0.0	0.1066	0.0170	0.0221	0.0640
Amsterdam	0.1931	0.10	0.0951	0.0175	0.0241	0.0699
T704	0.1780	0.56	0.1045	0.0174	0.0171	0.0722
Peter Pears	0.1738	0.76	0.0886	0.0168	0.0229	0.0726
Green Star	0.1509	0.83	0.0747	0.0160	0.0203	0.0851
Jester	0.1429	1.55	0.0870	0.0157	0.0188	0.0653
White Goddess	0.1736	0.75	0.0985	0.0158	0.0256	0.0563
Gold Field	0.1666	2.42	0.0896	0.0135	0.0244	0.0627

ing the Root Mean Square Error (RMSE) between observed and simulated CLN values:

$$RMSE = \left[\sum (Si\text{-}Oi)^2/n\right]^{0.5} \qquad (6)$$

where Si = simulated CLN values, Oi = observed CLN values and n = number of observations. The unit of RMSE is the same of Si and Oi, that is, leaves per plant.

The coefficients rmax$_s$, rmax$_v$, rmax$_h$, and rmax$_f$ were parameterized for each developmental phase (PL-VE, VE-R1) and sub-phase (R1-R2, R2-R5), respectively, with SAS (SAS Institute, 2001) using the NLIN procedure and the Marquardt method.

2.10. Model evaluation

The temperature response function of the sprouting phase was evaluated with the independent data collected in the temperature treatments of 7 °C, 16 °C, and 30 °C of the controlled environmental experiment. The evaluation of the model in simulating CLN and the developmental stages was with data collected in the field experiments that were not used for model parameterization (Table 2), which were independent data. For each planting date, cultivar and location, the model was run twice: one run started at planting date and the other run started at emergence date. The reason for these two runs is that for practical applications both dates can be used
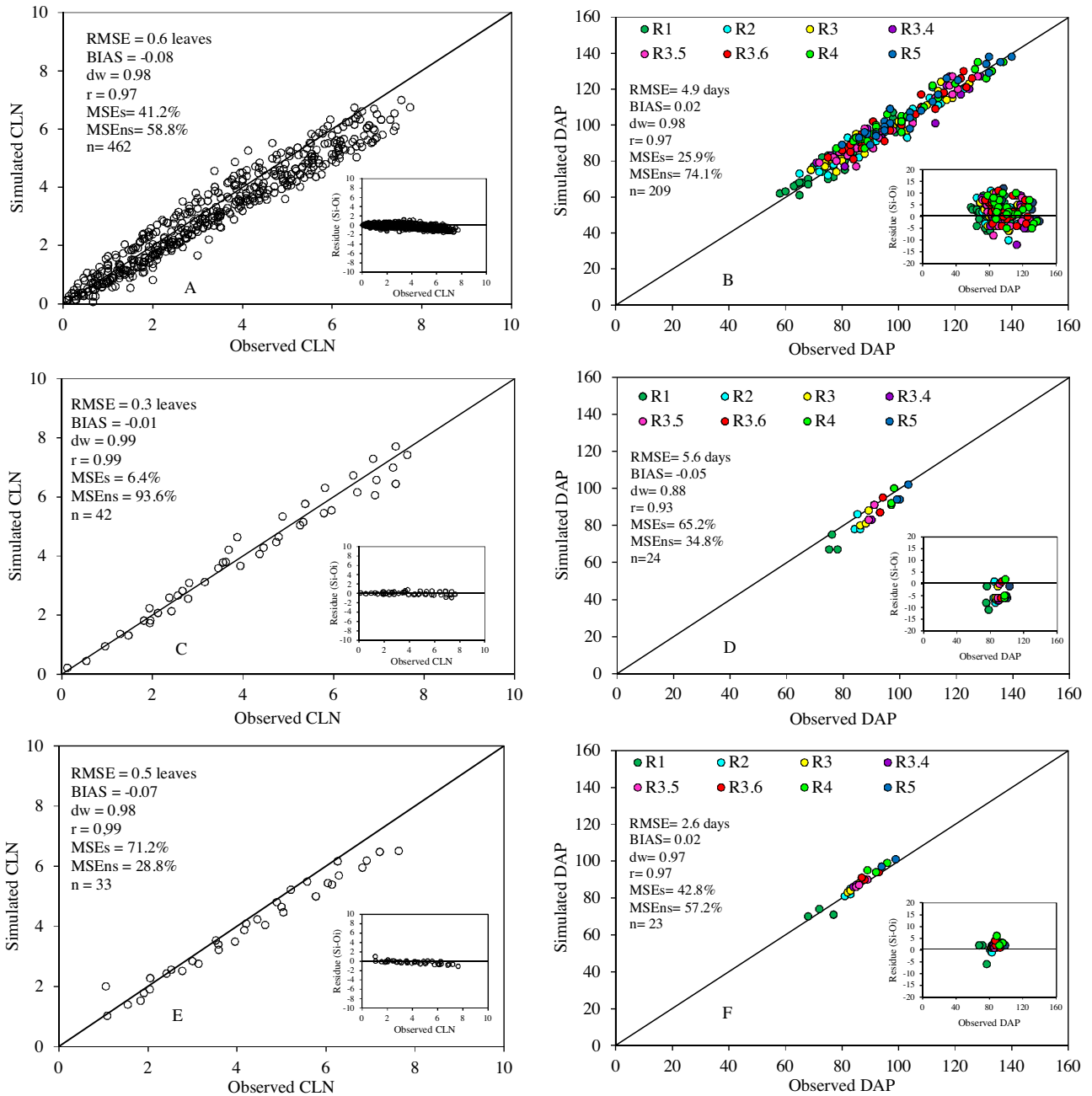
Fig. 5. The simulated versus observed cumulative leaf number (CLN) (panels A, C and E) and the simulated versus observed days after planting (DAP) of heading (R1), blooming (R2), onset of anthesis (R3), half of anthesis (R3.4), beginning floret senescence (R3.5), half of florets senesced (R3.6), anthesis completed (R4) and, end of floret senescence (panels B, D and F) for Gladiolus cultivar Jester in three locations in Rio Grande do Sul State, Brazil (Santa Maria: panels A and B, Itaqui: panels C and D, Frederico Westphalen: panels E and F) with the PhenoGlad model. Data of all planting dates are pooled. The solid line is the 1:1 line. Insets are the residuals. RMSE = root mean square error, BIAS = BIAS index, dw = index of agreement, r = correlation coefficient, MSEs = percentage of systematic means square error, MSEns = percentage of unsystematic mean square error, n = number of observations.

to run the model. The ability of the PhenoGlad model to simulate the developmental stages of harvested spikes in the six Gladiolus cultivars was with the data collected in the postharvest experiment (vase life). For this experiment, the model was run starting at R2 (the day when the spikes were harvested).

Model performance was evaluated with the statistics RMSE (Eq. (6)), BIAS index (Wallach, 2006), index of agreement (dw) (Willmott, 1981), correlation coefficient (r) and systematic (MSEs) and unsystematic (MSEns) errors (Willmott, 1981). Low RMSE, close to zero BIAS, close to one dw and r, and low systematic and

high unsystematic error are characteristics of a good model. The equations to calculate each of these statistics are:

$$BIAS = \left(\sum S_i - \sum O_i \right) / \sum O_i \tag{7}$$

$$dw = 1 - \left[\sum \left(S_i - O_i \right)^2 \right] / \left[\sum \left(|S_i - \bar{O}| \right) + \left(|O_i - \bar{O}| \right) \right]^2 \tag{8}$$

$$r = \sum \left(O_i - \bar{O} \right) \left(S_i - \bar{S} \right) / \left\{ \left[\sum \left(O_i - \bar{O} \right)^2 \right] \left[\sum \left(S_i - \bar{S} \right)^2 \right]^{0,5} \right. \tag{9}$$

$$MSEs = \left[\sum (\hat{S}_i - O_i)^2 \right] / n \tag{10}$$
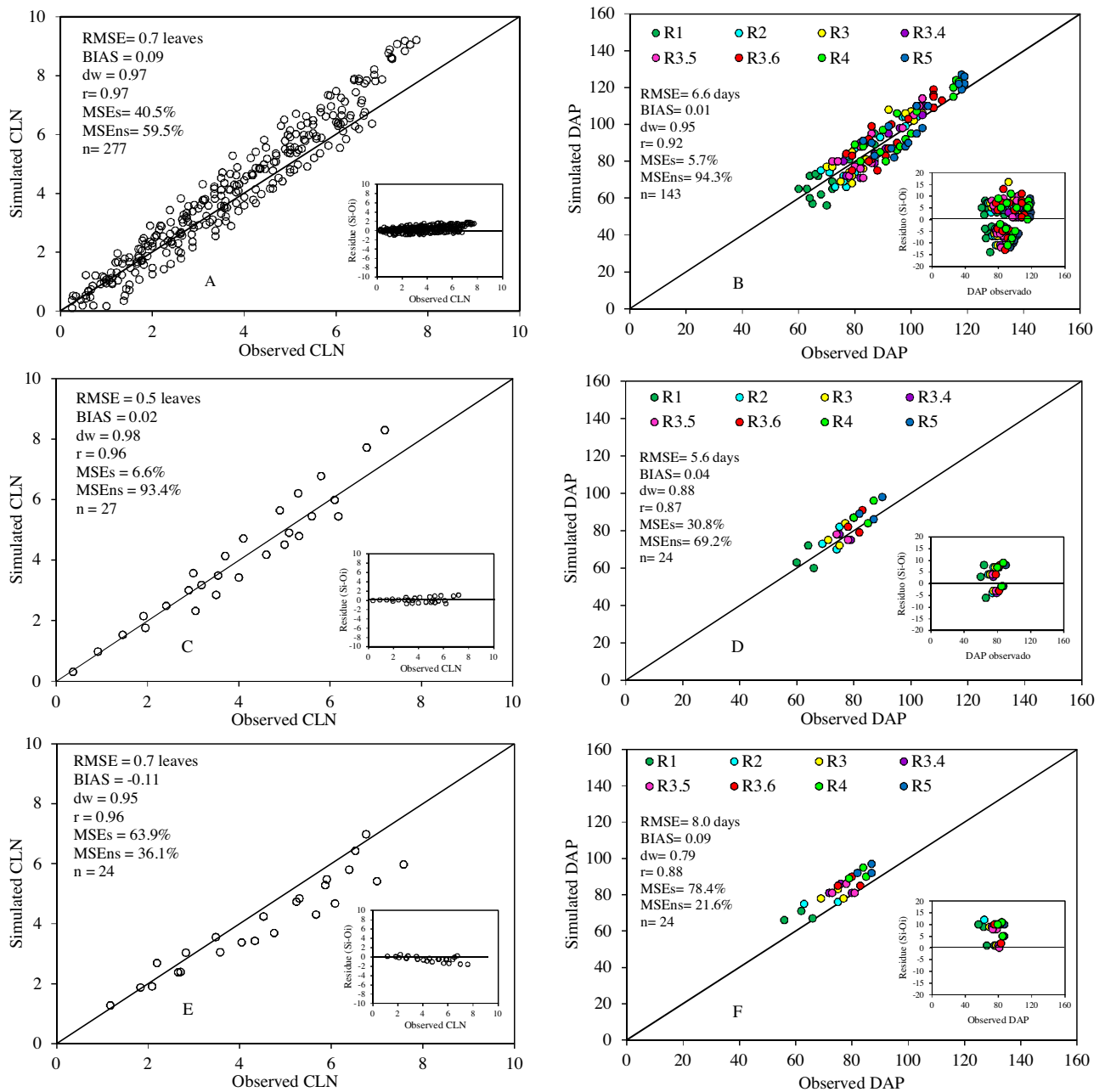
Fig. 6. The simulated versus observed cumulative leaf number (CLN) (panels A, C and E) and the simulated versus observed days after planting (DAP) of heading (R1), blooming (R2), onset of anthesis (R3), half of anthesis (R3.4), beginning floret senescence (R3.5), half of florets senesced (R3.6), anthesis completed (R4) and, end of floret senescence (panels B, D and F) for Gladiolus cultivar Rose Friendship in three locations in Rio Grande do Sul State, Brazil (Santa Maria: panels A and B, Itaqui: panels C and D, Frederico Westphalen: panels E and F) with the PhenoGlad model. Data of all planting dates are pooled. The solid line is the 1:1 line. Insets are the residuals. RMSE = root mean square error, BIAS = BIAS index, dw = index of agreement, r = correlation coefficient, MSEs = percentage of systematic means square error, MSEns = percentage of unsystematic mean square error, n = number of observations.

$$MSEns = \left[\sum (Si - \hat{S}i)^2 \right] / n \qquad (11)$$

where S_i are the simulated values, S is the mean of the simulated values, O_i are the observed values, $\bar{O}$ is the mean of the observed values, n is the number of observations, and $\hat{S}i = a + b(O_i)$ with a and b being the intercept and the slope of the linear regression of S_i against O_i, respectively.

The evaluation of the model in simulating chilling and heat injuries was with the 2×2 Contingency Table approach (Wilks,

2006). In this approach, model accuracy (PC) in forecasting a discrete event was calculated as:

$$PC = (Y + N)/n \qquad (12)$$

where Y is the number of predicted events, N is the number of non-predicted events and n is the total number of observed events and no events.
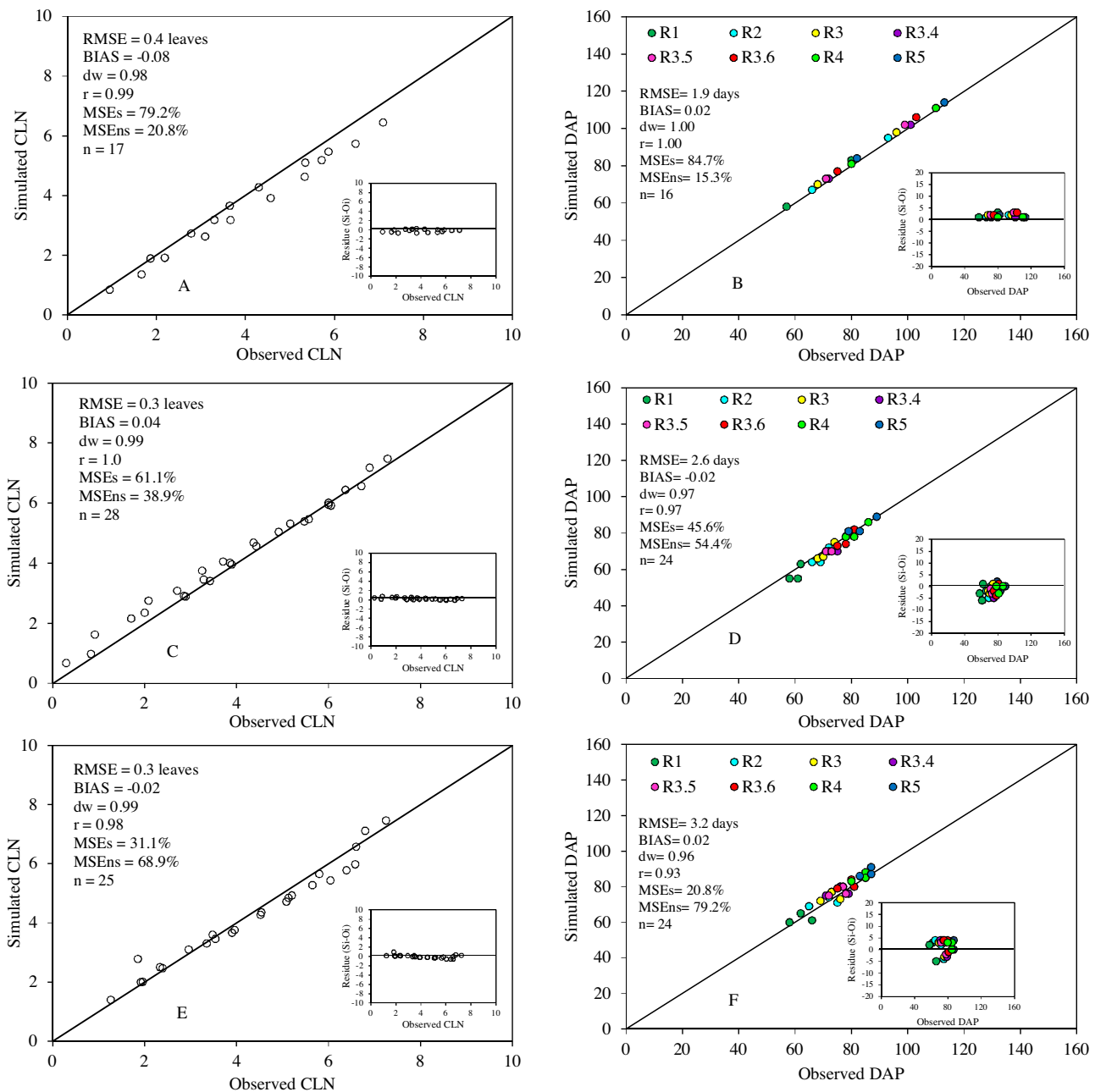
Fig. 7. The simulated versus observed cumulative leaf number (CLN) (panels A, C and E) and the simulated versus observed days after planting (DAP) of heading (R1), blooming (R2), onset of anthesis (R3), half of anthesis (R3.4), beginning floret senescence (R3.5), half of florets senesced (R3.6), anthesis completed (R4) and, end of floret senescence (panels B, D and F) for Gladiolus cultivar White Friendship in three locations in Rio Grande do Sul State, Brazil (Santa Maria: panels A and B, Itaqui: panels C and D, Frederico Westphalen: panels E and F) with the PhenoGlad model. Data of all planting dates are pooled. The solid line is the 1:1 line. Insets are the residuals. RMSE = root mean square error, BIAS = BIAS index, dw = index of agreement, r = correlation coefficient, MSEs = percentage of systematic means square error, MSEns = percentage of unsystematic mean square error, n = number of observations.

2.11. Model coding and software

The model was coded in FORTRAN 77 and a friendly interface was built in Java (version 1.8.0_66). Version 1.0 of PhenoGlad is available for free by contacting the authors.

3. Results

3.1. Meteorological conditions during the field experiments

There was a large variation in weather conditions during the nine experiments (Table 3). In general, solar radiation was higher in the Spring and Summer months and precipitation was well distributed throughout the year. In Santa Maria, Experiment 3 was the warmest, with the highest maximum air temperature of 40.2 °C in February 2014. The lowest minimum air temperature was in Autumn 2012 (−2 °C), during Experiment 1. Among the other three locations, Itaqui was the warmest, with maximum temperature reaching 37.5 °C during Spring 2014, and Curitibanos was the location with the lowest temperature (highest maximum temperature during Spring was 31.5 °C). The distinct meteorological conditions among different planting dates and locations provide a rich data set to parameterize and evaluate the PhenoGlad model.
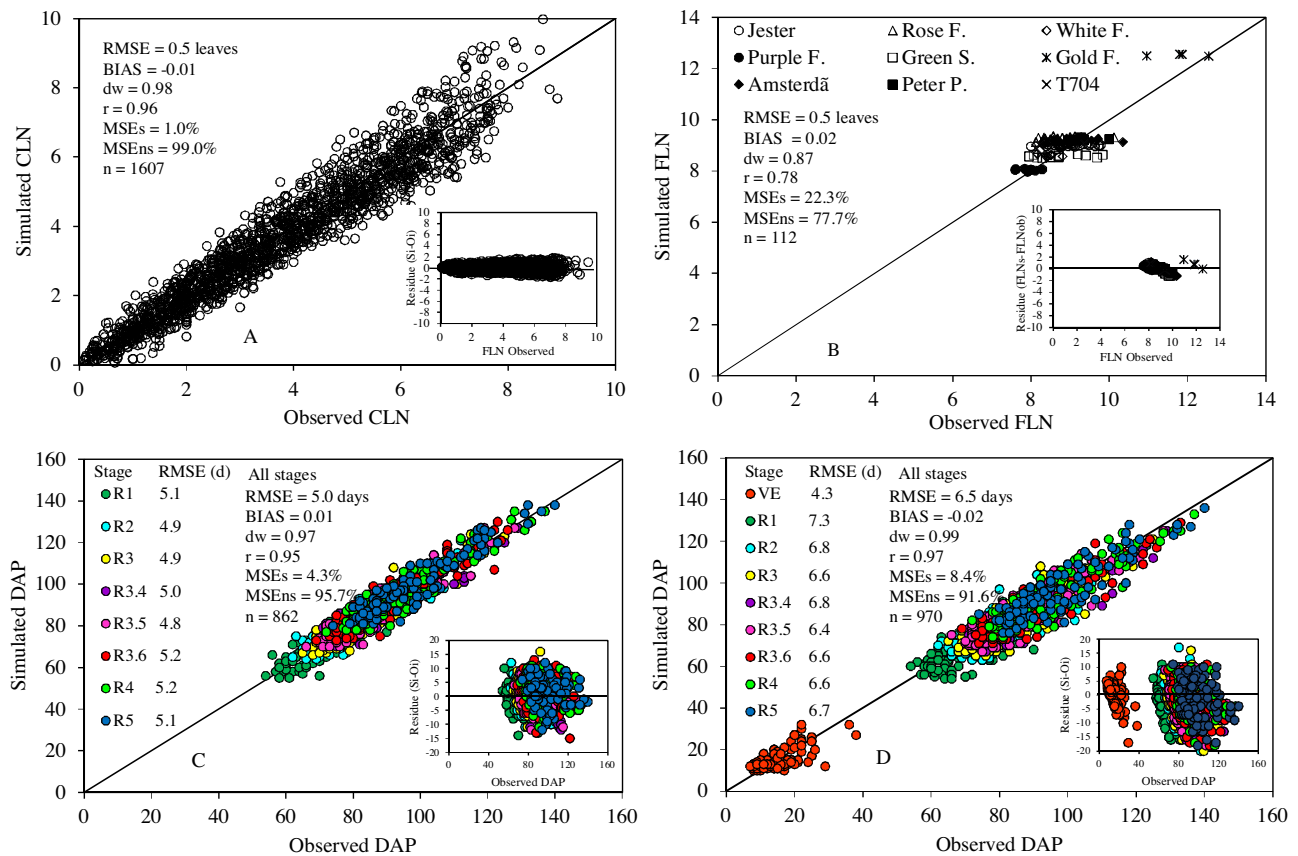
Fig. 8. The simulated versus observed cumulative leaf number (CLN) (A), final leaf number (FLN) (B), and days after planting (DAP) with the PhenoGlad model starting at emergence (C) and days after planting (DAP) with the PhenoGlad model starting at planting (D) of the developmental stages emergence (VE), heading (R1), blooming (R2), onset of anthesis (R3), half of anthesis (R3.4), beginning floret senescence (R3.5), half of florets senesced (R3.6), anthesis completed (R4) and end of floret senescence (R5) in Gladiolus. Data of 10 cultivars, three locations in Rio Grande do Sul State (Santa Maria, Itaqui and Frederico Westphalen) and several planting dates are pooled. The solid line is the 1:1 line. Insets are the residuals. RMSE = root mean square error, BIAS = BIAS index, dw = index of agreement, r = correlation coefficient, MSEs = percentage of systematic means square error, MSEns = percentage of unsystematic mean square error, n = number of observations.

3.2. Estimates of model coefficients

The estimates of LAR_{max}, CF, $rmax_v$, $rmax_h$ and $rmax_f$ for the ten gladiolus cultivars are in Table 4. There was small variation in the LAR_{max} and $rmax_s$ among cultivars and greater variation of CF, $rmax_v$, $rmax_h$ and $rmax_f$ among cultivars. The $rmax_v$ is the coefficient more correlated with the length of the developmental cycle, with early cultivars having the smallest while late cultivars have the largest $rmax_v$.

3.3. Temperature response function for the sprouting phase

The emergence rates of the cultivar Amsterdam at 7 °C, 16 °C and 30 °C in the controlled experiment were well described by the temperature response function f(T) (Fig. 4). The emergence rates measured at 16 °C and 30 °C are similar, indicating supra optimal effects on emergence in the latter. Emergence rate measured at 7 °C is very low as this temperature is near the lower base temperature assumed in the model (5 °C).

3.4. Simulation of leaf appearance and final leaf number

Simulated versus observed cumulative leaf number (CLN) for the independent data simulated with the PhenoGlad model are presented in Fig. 5A, C, and E (for cultivar Jester, experiments in Santa Maria, Itaqui, and Frederico Westphalen, respectively), Fig. 6A, C, and E (for cultivar Rose Friendship in the three locations) and Fig. 7A, C, and E (for cultivar White Friendship in the three loca-

tions). For other cultivars in the three locations see Supplementary information (Figs. S1–S4). The Root Mean Square Error (RMSE) varied from 0.4 leaves for cultivars White Friendship, Purple Flora and Peter Pears up to 0.8 leaves for cultivar Green Star in Santa Maria. In Itaqui, the RMSE varied from 0.2 leaves for cultivar Purple Flora and Green Star up to 0.6 leaves for Gold Field and in Frederico Westphalen, the RMSE varied from 0.3 leaves for White Friendship, Purple Flora, Green Star and Gold Field up to 0.7 leaves for Rose Friendship cultivar.

Pooling all data (cultivar x planting dates x years x locations), the RMSE was 0.5 leaves for the CLN (Fig. 8A). Decomposing the RMSE into systematic (MSEs) and non-sistematic (MSEns) percentage components (Willmott, 1981), the MSEs was 1% and the MSEns was 99.0%. The RMSE for leaf number in wheat and rice with the Wang and Engel model (Eq. (1)) varied from 0.3 to 0.7 leaves (Streck et al., 2003b,2008), indicating that the PhenoGlad model had good performance in simulating leaf development. The BIAS index was close to zero and the dw and r were high, with values of 0.98 and 0.96, respectively. For final leaf number (Fig. 8B), the RMSE was 0.5 leaves, systematic and non-systematic errors were 22.3% and 77.7%, respectively, and the dw and r indexes were 0.87 and 0.78, respectively.

3.5. Simulation of developmental stages

Simulated versus observed days after planting (DAP) for the independent data of heading (R1), blooming (R2), onset of anthesis (R3), half of anthesis (R3.4), beginning floret senescence (R3.5),
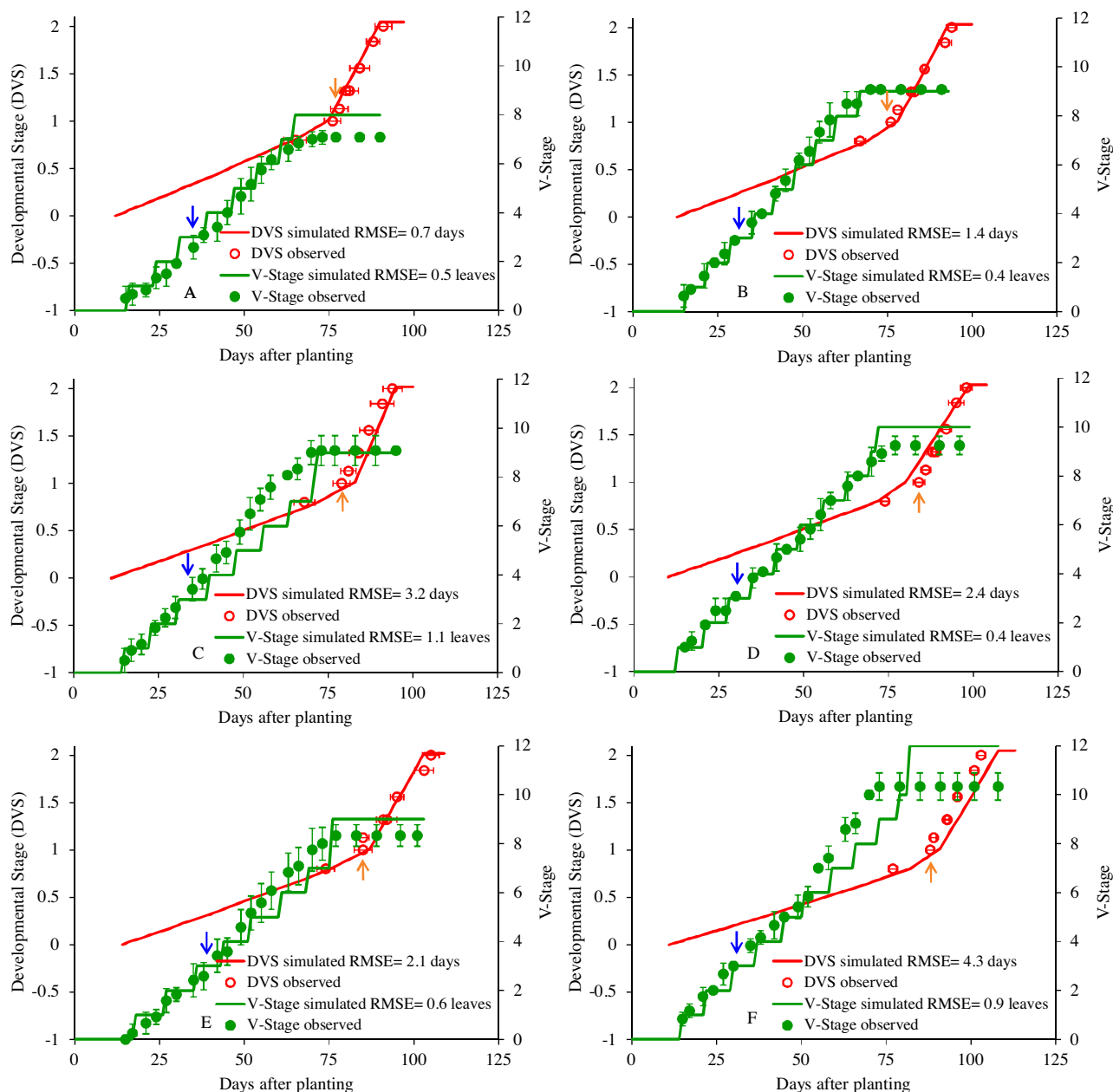
Fig. 9. Developmental stage (DVS) and V-Stage as a function of days after planting for six Gladiolus cultivars (A = Purple Flora, B = Amsterdam, C = Green Star, D = White Goddess, E = Jester, F = Gold Field) grown in Curitibanos, SC, Brazil, as observed and simulated with the PhenoGlad model run from emergence. Arrows represent the timing of nitrogen side dressing at V3-stage (blue arrow) and harvest point (orange arrow). Planting date was on 29 September. 2015. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

half of florets senesced (R3.6), anthesis completed (R4) and end of florets senescence (R5) for each Gladiolus cultivar simulated with the PhenoGlad model run from emergence are presented in Fig. 5B, D, and F (for cultivar Jester, experiments in Santa Maria, Itaqui, and Frederico Westphalen, respectively), Fig. 6B, D, and F (for cultivar Rose Friendship in the three locations) and Fig. 7B, D, and F (for cultivar White Friendship in the three locations). For other cultivars in the three locations see Supplementary information (Figs. S1–S4). The RMSE varied from 1.9 days for the cultivar White Friendship to 6.6 days for the cultivar Rose Friendship in Santa Maria. In Itaqui, the RMSE varied from 2.6 days for cultivar White Friendship to 7.3 days for Gold Field cultivar. In Frederico Westphalen, the RMSE varied from 2.6 days for Jester up to 8 days for Rose Friendship cultivar.

Pooling all data (cultivars x planting dates x years x locations), when the model started at emergence (Fig. 8C), RMSE for R-stages

varied from 4.8 to 5.2 days whereas when the model started from planting (Fig. 8D), the RMSE was higher (6.4–7.3 days). Overall, other statistics (BIAS, dw, r, MSEs and MSEns) were slightly better when the model started from emergence (Fig. 8C) compared to when the model started from planting (Fig. 8D). A slightly greater error in simulating the R-stages when PhenoGlad was run from planting was because the model had an average error of 4.3 days to predict emergence (VE).

3.6. Performance of the PhenoGlad model in Santa Catarina State

The experiment in Curitibanos is an important dataset as this site is located in high altitude (992 m.a.s.l.), and temperature is quite different from the other three locations. In both planting dates, the observed duration of the sprouting phase was
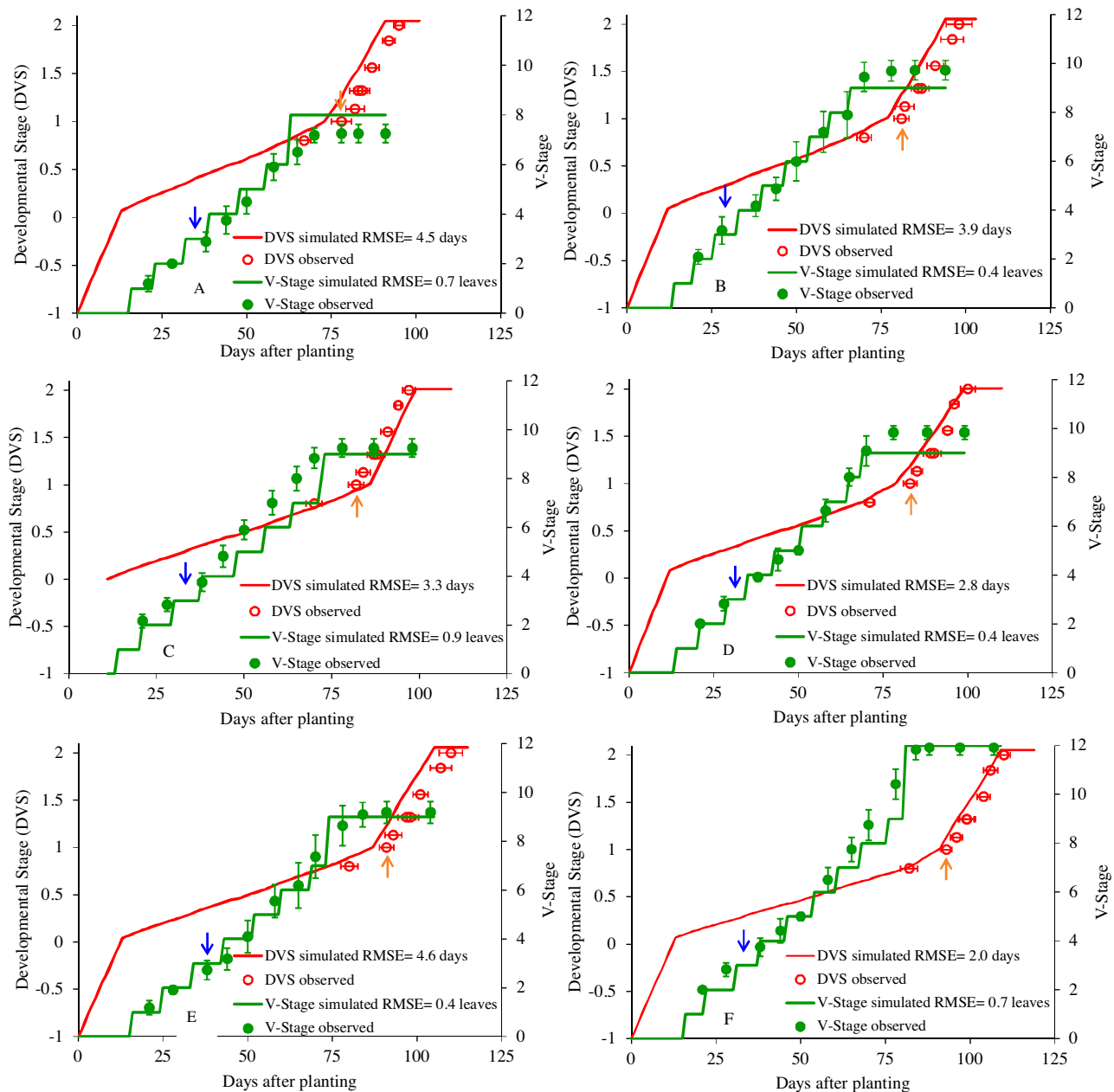
Fig. 10. Developmental stage (DVS) and V-Stage as a function of days after planting for six Gladiolus cultivars (A = Purple Flora, B = Amsterdam, C = Green Star, D = White Goddess, E = Jester, F = Gold Field) grown in a commercial farm in Santa Maria, RS, Brazil, as observed and simulated with the PhenoGlad model. The model was run from planting for all cultivars, except for cultivar Green Star, for which the model was run from emergence. Arrows represent the timing of nitrogen side dressing at V3-stage (blue arrow) and harvest point (orange arrow). Planting date was on 27 July 2015. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shorter (10–15 days) than the simulated by the model (15–20 days), because other factors affected the sprouting rate besides air temperature. Because of this, the model was run for Curitibanos by setting the observed emergence day. Model performance in simulating the V-stages and the R-stages of the six cultivars planted on 29 September 2015 was good, with RMSE for the R-stages varying from 0.7 to 4.3 days (Fig. 9). For the 30 October 2015 planting date, model performance for the R-Stages was with an RMSE varying from 4.3 to 8.1 days (data not shown). As an application of the model for field management practices, arrows in panels of Fig. 9 indicate the recommended timing of nitrogen side dressing (blue arrow) at V3 (Schwab et al., 2015) and the harvest point (orange arrow).

3.7. On-farm performance of the PhenoGlad model

The ability of PhenoGlad in simulating the V-stages and R-stages of the six Gladiolus cultivars grown in a commercial farm is in Fig. 10. The model was run from planting date except for cultivar Green Star (Fig. 10C), for which the model was run from observed emergence date because the observed sprouting phase was badly predicted by the model (emergence day was 4 days earlier than the simulated day), and we were not able to find a plausible explanation for the poor performance for the sprouting phase. The V-stages and FLN were accurately simulated by the PhenoGlad model, with RMSE varying from 0.4 leaves for Amsterdam, White Goddess and Jester cultivars up to 0.9 leaves for Green Star cultivar (Fig. 10B–E).

Table 5
Percentage of model accuracy (PC), for predicting chilling and heat injuries with the PhenoGlad model in Gladiolus grown in Santa Maria and Frederico Westphalen, RS, Brazil. n = number of observations.

Location	Chilling		Heat injury	
	PC (%)	n	PC (%)	n
Santa Maria	100	27	77.7	40
Frederico Westphalen	–	–	95.6	23

The RMSE for the developmental stages varied from 2.0 days for Gold Field to 4.6 days for Jester (Fig. 10F and E).

Analysing the developmental cycle of each cultivar, Purple Flora and Amsterdam cultivars were earlier (Fig. 10A and B) whereas Gold Field had the longest developmental cycle (Fig. 10F). These results are important for the selection of the appropriate cultivar and adjusting planting dates of different cultivars when the goal is to sell Gladiolus spikes on specific holidays such as All Souls' Day and Mother's day, the two most important holidays for marketing Gladiolus in Brazil.

3.8. Simulation of developmental stages in harvested spikes

The performance of the PhenoGlad model for simulating the developmental stages (from R3 to R3.6) of Gladiolus spikes during the vase life is showed in Fig. 11. The RMSE was 1.3 days and other statistics (BIAS = 0.03, dw = 0.94, r = 0.89, MSEs = 15.8%, MSEns = 84.2%) show good performance and indicate that the model has application for postharvest conditions.

3.9. Simulation of chilling and heat injury

The model accuracy (PC) to predict chilling in Gladiolus spikes in the field experiments conducted in Santa Maria during Autumn and Winter was 100% (Table 5). Most of the plants of Gladiolus cultivars other than Jester (used for parameterization) planted on 02 April 2012 were at the heading sub-phase when lethal temperatures occurred. The plants of all cultivars from an earlier planting date (07 March 2012) were at the flowering sub-phase on the day that field temperature reached −2 °C, and florets opening process stopped. The evaluation of the high temperature warnings (risk of severe burning on the Gladiolus spikes) was with model accuracy (PC) of 77.7% in Santa Maria and 95.6% in Frederico Westphalen (Table 5).

3.10. Using PhenoGlad to simulate genotype x environment interactions

As an application of the model for simulating genotype x environment interactions on Gladiolus phenology, we run the model for nine cultivars, three locations (Santa Maria, Itaqui and Frederico Westphalen) and three planting dates (30 July 2014, 30 August 2014, and 30 September 2014) from planting to harvest point (Fig. 12). The vegetative phase (VE-R1, green bars), is the longest phase whereas heading (R1-R2, open bars) is the shortest phase. The later the planting date, the shorter the developmental cycle because of increase in temperature as planting date is delayed from July to September. Among cultivars, White Friendship, Purple Flora, Rose Friendship and Amsterdam are the earliest to flower whereas Gold Field is the latest. Differences among locations were not evident for these three planting dates. The model also simulated injuries on sepals due to high temperature during the reproductive phase before harvest for the 30 July 2014 planting date in Santa Maria and Itaqui (red bars).
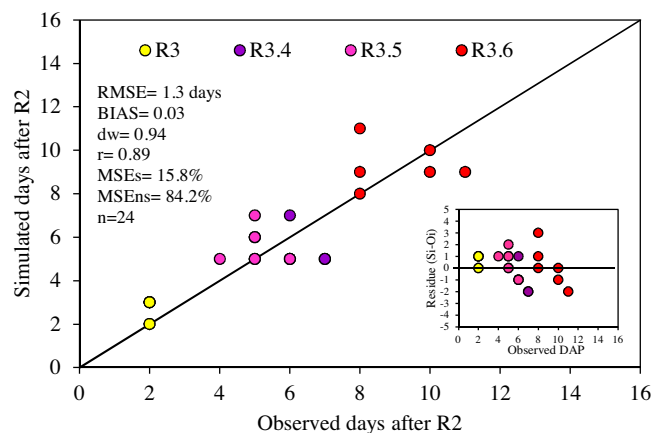

Fig. 11. The simulated versus observed days after harvest of onset of anthesis (R3), half of anthesis (R3.4), beginning floret senescence (R3.5) and half of florets senesced (R3.6) in harvested spikes of six Gladiolus cultivars: Purple Flora, Amsterdam, White Goddess, Green Star, Jester and Gold Field with the PhenoGlad model. The solid line is the 1:1 line. Inset is the residuals. RMSE = root mean square error. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

The different cultivars, planting dates, and locations (Table 1) led plants to grow under distinct temperatures and soils. This is important in order to test the robustness of PhenoGlad in simulating the timing of developmental stages under conditions different from the parameterization environments. PhenoGlad uses a non-linear response function (Eqs. (2), (3)) to describe the temperature effects on the rate of development. This approach has been successfully used to simulate the phenology and LAR in winter wheat (Wang and Engel, 1998; Streck et al., 2003a,b; Xue et al., 2004), rice (Streck et al., 2008, 2011), maize (Streck et al., 2009), soybean (Setiyono et al., 2007), potato (Streck et al., 2007), sweet potato (Erpen et al., 2013) and cassava (Samboranha et al., 2013), and has now been successfully applied to Gladiolus with the PhenoGlad model.

The genotype-specific coefficients of the PhenoGlad model (LAR_{max}, $rmax_s$, $rmax_v$, $rmax_h$, $rmax_f$) have biological meaning and operational definition (can be actually measured). They represent the maximum development rate (or the shortest duration of a developmental phase), which is attained at optimum temperature. At suboptimal and at supraoptimal temperatures, the rate of development decreases, reaching zero at Tb and TB, respectively (Fig. 3). This response is based on fundamental relationships between the rate of biological processes and temperature (Schaykewich, 1995).

PhenoGlad showed good performance among cultivars, planting dates, years, and sites, as indicated by the low RMSE values (Fig. 5–10). The value of RMSE for CLN was lower than 1 leaf (Figs. 5–7, S1–S4), which is lower than in other crops like potato, with RMSE = 2.0 leaves (Streck et al., 2007), sweet potato, RMSE = 2.2 leaves (Erpen et al., 2013), and cassava, RMSE = 3.2 leaves (Samboranha et al., 2013). An error of one leaf in Gladiolus is acceptable for practical applications. For instance, nitrogen top dressing is recommended between V3 and V4, so an error of one leaf would not affect the efficiency of nitrogen application. The RMSE in the prediction of developmental stages varied from 4 to 5 days (Fig. 8C), which is similar to the RMSE with the WE model for other crops, such as 3.3–3.8 days for soybean (Setiyono et al., 2007), 7 days for potato (Streck et al., 2007), 4.3–10.9 days for rice (Streck et al., 2011), 2.7–4.8 days for maize (Streck et al., 2009) and 5–6 days for winter wheat (Streck et al., 2003a). For practical applications, an error of five days for developmental stages is acceptable in Glad-
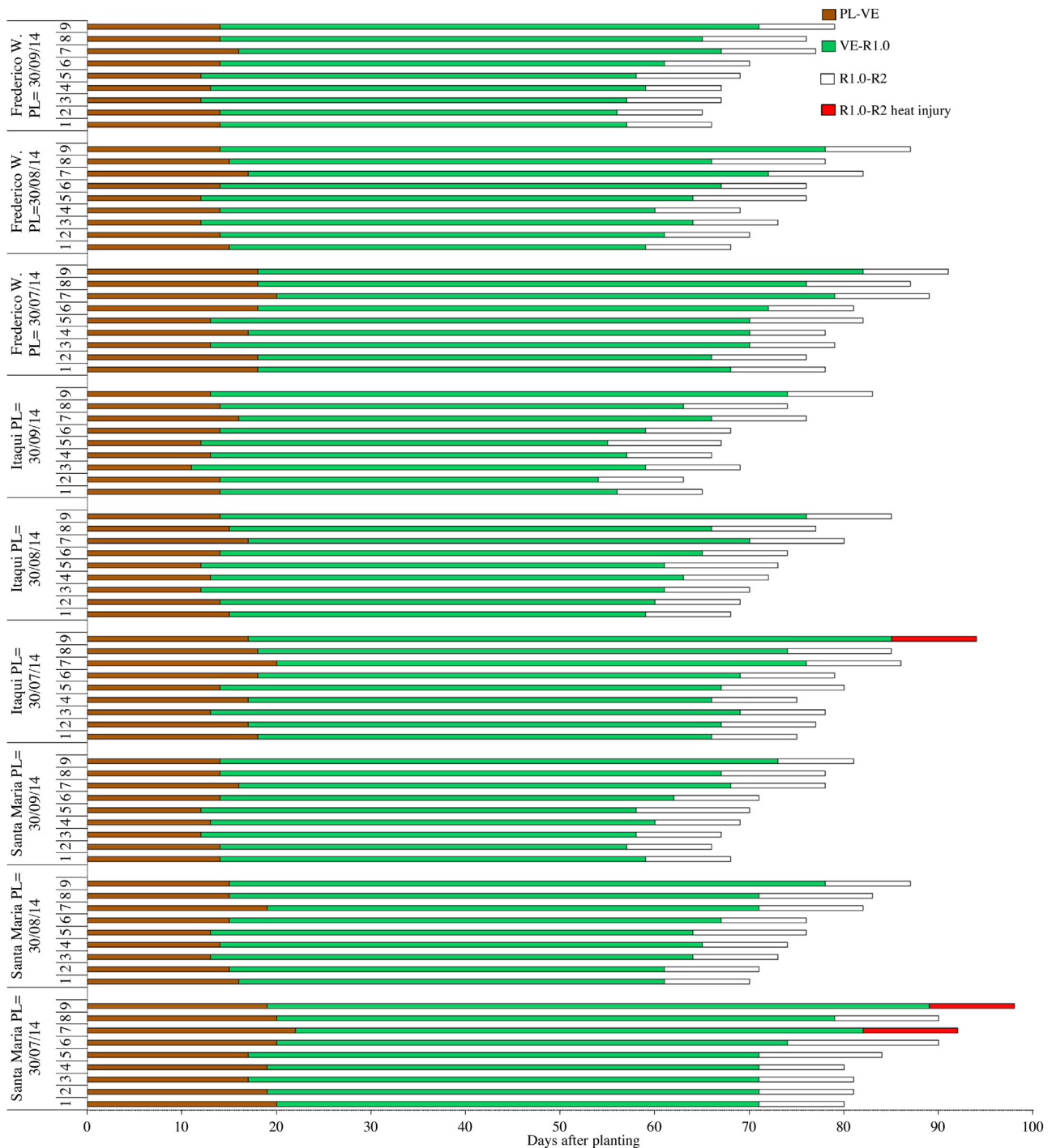
Fig. 12. Duration (days) of the developmental phases planting to emergence (PL-VE), emergence to heading (VE-R1.0), and heading to flowering (R1.0-R2), of nine Gladiolus cultivars (1 = White Friendship, 2 = Purple Flora, 3 = Rose Friendship, 4 = Amsterdam, 5 = T704, 6 = Peter Pears, 7 = Green Star, 8 = Jester and 9 = Gold Field) simulated with the PhenoGlad model for three planting dates (30 July 2014, 30 August 2014, and 30 September 2014) in Santa Maria, Itaqui and, Frederico Westphalen, RS, Brazil. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

iolus. For example, if the model predicts the flowering time before a target marketable day, the farmer still can cold store the spikes (5–8 °C) for up to 15 days, slowing down the progress of flower opening so that spikes are marketable at the target day.

The accuracy of the PhenoGlad model in simulating the developmental stages was lower when the model was run from planting compared to when the model was run from emergence date (Fig. 8C, D). This is not surprising as sprouting is driven only by temperature in PhenoGlad (Fig. 2a) and we hypothesize that other factors

like soil type, soil temperature (instead of air temperature), planting depth, and internal factors of the corm that affect the degree of sprouting at planting may contribute to sprouting rate. This part of the model (sprouting phase) needs further refining.

An important characteristic for consumers is the vase life of Gladiolus, which lasts from R3 to R4 developmental stages. PhenoGlad was able to simulate the vase life with an average error of one day (Fig. 11). Additionally, the model can be used to simulate the florets opening rate during storage under lower temperatures

and to predict the storage time. For instance, at 8 °C the estimated time from R3 (first open floret) to R4 (last open floret) is 62 days whereas at 10 °C the estimated time is 31 days.

Gladiolus spikes quality is affected by planting dates (Zubair et al., 2006). Planning harvest time is critical for flower crops and models can be useful tools for defining the planting dates for different cultivars to be ready for harvesting at the right time. For instance, PhenoGlad can be used to define regions and seasons where the risk of low and high temperatures injuries is minimal (agricultural zoning). A further use of PhenoGlad is to predict the optimal planting date for cultivars of different developmental cycles aiming to harvest the spikes for selling at specific holidays.

There is no consensus in the literature about the effect of photoperiod on Gladiolus. Some authors argue that Gladiolus is a facultative short day plant (Shillo and Halevy, 1976b) and long photoperiods (beyond 12 h) after emergence or at the 4–leaf stage increased the number of florets per spike, the length of spike and flower stalk, but delayed flowering time (Shillo et al., 1981). On the other hand, short photoperiods at this stage accelerated flowering time, but decreased the accumulation of photosynthates, by reducing the growing period (Salunkhe et al., 1990). We tested the hypothesis of photoperiod affecting the timing of developmental stages of the Gladiolus cultivars used in this study by including a photoperiod response function for short day plants (Gao et al., 1992) in the model during the vegetative phase, but there was no improvement in the simulations (data not shown), indicating that photoperiod was not a major factor affecting the development of these Gladiolus cultivars.

5. Conclusions

We proposed a model for simulating the vegetative and reproductive development of Gladiolus, named PhenoGlad. The model was able to simulate the Gladiolus phenology across a wide range of cultivars, planting dates, years and locations, irrigated and rainfed experiments, including an on-farm experiment. PhenoGlad was also efficient in predicting the effects of chilling and high temperatures damage on florets and in simulating the vase life of Gladiolus spikes. The PhenoGlad model can be used for practical applications, as data inputs requirement are only minimum and maximum temperature, cultivar and planting date or emergence date.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.eja.2016.10.001.

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