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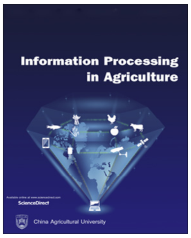

Herbaceous peony in warm climate: Modelling stem elongation and growers profit responses to dormancy conditions

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ABSTRACT

We analysed the data collected for herbaceous peony cultivated in a warm climate region and stored in winter under three constant chilling temperatures. We used the quadratic regression model to describe the stem elongation responses to winter dormancy conditions, and the logistic function to describe the weekly stems elongation. The predicted maximal stem length from the first model was used as the input parameter for the second model. More than 4000 data for various (a) chilling constant temperatures during dormancy, (b) dormancy duration, and (c) germination duration, were used. The models were applied to determine the optimal number of chill units. For this purpose, two criteria were used in different versions of the model: the maximal stem length and the maximal profit of farmers. For the two chilling temperatures of 2 °C and 6 °C, the optimal values of chill units (in the models of a maximal stem length and maximal profit of farmers) are close to one another, and the values of a maximal stem length and maximal profit are significantly different. In the case of the third chilling temperature of 10 °C, the model failed to determine the optimal number of chill units. The method of inverse confidence intervals for testing the significance of the optimal number of chill units was used.

1. Introduction

Most of the traditional geophyte flowers are cultivated in temperate-climate regions. As the global demand for these flowers increases, new efforts to search for and introduce new climatic regions for their production are made [1]. In the last time, peony became an important commercial geophyte flower crop. In FloraHolland, the largest flower auction in the world, peony are ranked 12th among the cut flowers with the 2013 turnover in this auction amounting to € mln 32 for 72 mln sold units. This flower when grown in Europe stands in the flower calendar for weeks 18/19 – 23 (end April–beginning June) [2]. Grown in warm climate regions, peony flowers have high potential in the international market in early spring [3]. Like for other geophyte flowers, particularly growing in warm climate

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regions, proper temperature and duration of winter dormancy are required for optimal after dormancy release growth and synchronised flowering within a population [4,5]. Various chilling and pre-chilling regimes are investigated for the purpose of extending the flowering season [6].

1.1. *Related research*

What are the main parameters of the optimal growth of geophytes, and particularly, peony, in regards to their stem elongation and other phenological characteristics in warm climate regions? How can these parameters be estimated related to dormancy conditions and duration? These questions are not sufficiently researched in the literature. On the one hand, numerous recent studies have been reported about:

(a) Peony stem elongation responses on changes in dormancy temperature and duration comparing various constant chilling temperatures for different durations [7].
(b) After dormancy release sprouting and flowering of Solomon's seal for field or constant chilling temperatures for different chilling duration [8], the effect of exposing lily bulblets to different temperatures (for dormancy break) on plant growth [9], of cold storage duration of *Erythronium japonicum* Decne. (Liliaceae) bulbs on days to sprouting and percent sprouting [10], of storage duration and temperature of Nerine sarniensis on flowering time and flower quality [11].
(c) A possibility of increasing the availability of planting materials and improving the growth performance in cut flower (tuberose) due to low temperature treatment of bulbs with subsequent storage [12].
(d) A theoretical model of the influence of low temperature on the growth of geophytes [13].

On the other hand, published studies do not detail analytical procedures that could present "dormancy – stem elongation" relationships for geophytes in a mathematical form convenient for quantitative analysis. In particular, dynamic stem length models, by weeks of dormancy and stem elongation period, are not published. For other plants, the regression models of the elongation as a function of cool and warm temperature treatments are developed. In the study of Pi et al. [14] these models were successfully used for the estimation of germination of grass seeds.

1.2. *Novelty of the approach*

Optimal dormancy conditions can be defined as those which produce high quality plants in a short period of time [15]. For peony, stem length is one of the main characteristics that determine market quality and price of these flowers. In the modelling context, the maximal stem length and weekly growth rate can be considered as variables dependent on the chilling regime characteristics – temperature and duration. The novelty of our approach is that we can use the predicted (based on the chilling regime characteristics) maximal stem length as an input parameter in the model of stem growth during the elongation period. As an example of the practical importance of this approach we consider the problem of assessing the optimal chilling duration in terms of maximal profit of farmers. For this purpose we take into account chilling costs and peony price influenced by the stem length.

1.3. *Aims of the study*

Given the foregoing, the aims of this study are as follows: (a) develop statistical models of the peony maximal stem length dependent on dormancy conditions; (b) develop dynamic models of the peony weekly stem length and growth rate after dormancy release; and (c) test the models applicability to answer practical questions on determining chilling regimes profitable for farmers. In this study we use data collected during the large-scale treatments in northern Israel. The database is available at http://www.mop-zafon.org.il/files/DB18_Sept_2014.xlsx.

2. Materials and methods

2.1. *Data*

To estimate the models and test their applicability, we use the comprehensive database on peony development in warm climate. The database enables to study every single plant in its various physiological states, and it is large enough to estimate statistical models. It contains data collected during the dormancy and sprouting phases, in particular, data of stem elongation collected at the Avnei Eitan experimental station in northern Israel. In the experiments data of which are used in this study, rhizomes of *Paeonia lactiflora* cv. 'Sarah Bernhardt' were planted in containers, which were placed in October 2012 in cooling chambers at constant temperatures 2 °C, 6 °C, 10 °C (treatments 7, 8, 9, respectively). The full experimental design is detailed in our previous article [16]. In the present article, the data collected for peonies planted in natural soil (treatments 1–6) and not in containers, are not considered.

Soil temperatures measured at a depth of 5 cm were used for calculating chill units for every week of the dormancy phase [16]. Chill units were calculated according to [17,18].

After every week of chilling, six containers from each treatment were transferred to the greenhouse (release of dormancy and beginning of sprouting). The transfer of the containers continued for 15 weeks until February 2013. For each of the treatments 7 and 8, 910–930 measurements of stem length for various dormancy duration (3–17 weeks) and week of stem elongation (from 1 to 15) were used. The data of treatment 9 (742 measurements) were used only to verify that in most peony plants dormancy at a temperature of 10 °C does not allow receiving stems of the market length of at least 35 cm. The average maximum stem length was 16 cm for this treatment, and part of the stems that exceeded 35 cm, was only 8%.

2.2. *Modelling stem elongation responses to dormancy conditions*

The flow-chart in Fig. 1 depicts the sequence of modelling stages. The part A of the chart presents the input data used for modelling. The part B presents the modules for calculation needed to estimate the models and use them for the prediction of stems length. In every treatment the plants are exposed to a constant temperature in cooling chambers (module A1). In every week of dormancy, six plants are transferred from a cooling chamber to a greenhouse (release of dormancy). The amount of chill units accumulated before this week is used as an explanatory variable in a model of regression of a stem maximal length in the end of the stem elongation period (module B1). The model is estimated separately for every treatment because the treatments differ in their temperature regimes. The output *L* of the regression model can serve as an input parameter (more specifically, as an upper asymptote of the logistic function of growth) used in the model in the next phase of stem elongation (modules B2, B3). This model enables prediction of a stem length for various weeks of stem elongation (module B4).

2.3. *The model of a stem maximal length*

This model describes a stem maximal length *L* in the end of the stem elongation when *L* depends on the chilling period duration. To illustrate a possible practical application of this model, we present an example of the chilling duration which ensures the maximal profit of farmers. We assume that chilling conditions influence essentially peony stem elongation [19]. Our second assumption is that the too long chilling duration decreases the value of *L*. Therefore we use a quadratic regression model that allows the assumed curvature in the response of *L* on chill units *CU*. In this model, the criterion of the maximal value L^* of *L* determines the optimal duration of the chilling period (CU^*).

The quadratic regression model is defined as follows:

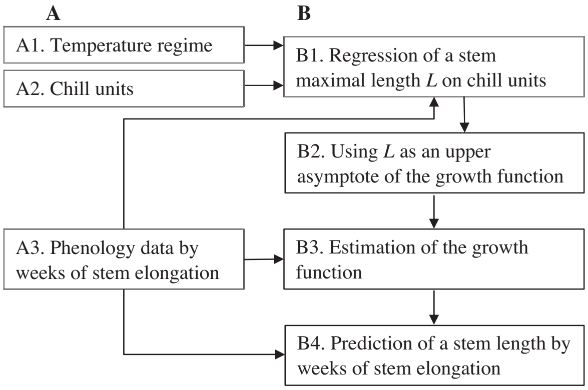

Fig. 1 – The flow-chart of dynamic modelling of stem elongation responses to conditions of dormancy in chilling chambers. A – input data: A1. Temperature in chilling chambers. A2. Chill units accumulated during the dormancy. A3. Phenology data can affect estimated parameters of the growth function. B – calculation modules: B1. Regressions (1), (5) of a stem maximal length on chill units. B2. The maximal stem length L serves an input parameter of the growth function. B3. The growth function (8) is estimated using this parameter. B4. A weekly stem length is predicted using the growth function.

$$Ln(L) = b_0 + b_1 Ln(CU) + b_2 (Ln(CU))^2 \tag{1}$$

where *CU* is chill units expressed in hours of chilling duration; *L* is a stem maximal length, in cm; and b_0, b_1, b_2 are the regression coefficients to be estimated. All variables are expressed in natural logarithms to reduce the effect of possible outliers.

The predicted stem maximal length L_{pred} is expressed as follows:

$$L_{pred} = \exp\left(b_0 + b_1 Ln(CU) + b_2 (Ln(CU))^2\right) \tag{2}$$

To illustrate how the model (1) can be applied to determine chilling regimes most profitable for farmers, we denote by *P* the part of the profit, which is dependent on the chilling cost and on the peony prices in flower auctions, in NIS per stem. This variable (hereinafter called "profit" for brevity) is defined as follows:

$$P = \mathrm{Price}_b + Price_{bonus} \cdot L_{pred} - C_f - C_v \cdot NW \tag{3}$$

where $Price_b$ is an assumed benchmark price received in flower auctions, in NIS/stem; the bonus $Price_{bonus}$ is added to the benchmark price; it has a value $Price_{<threshold}$ or $Price_{>threshold}$, in NIS/cm, depending on whether the stem is shorter or lengthier than some threshold for which the benchmark price is assumed; C_f is a fixed cost for the whole chilling period, in NIS/stem; C_v is a variable cost of chilling, in NIS/stem per one week of chilling; *NW* is the number of weeks of the chilling period. The relationship between *CU* and *NW* is determined as follows:

$$NW = CU/168 - 2 \tag{4}$$

where 168 is the total number of hours in a week.

In the first two weeks of the chilling period no plants were transferred to the greenhouse, and therefore the total chilling cost was referred to the fixed cost.

After estimating b_0, b_1, b_2 (Eq. (1)), calculating L_{pred} (Eq. (2)), *NW* (Eq. (4)), and calculating the profit *P* (Eq. (3)) for every value of chill units *CU* used in Eq. (1), the model of the quadratic regression of farmers' profit on chill units is defined as follows:

$$P = d_0 + d_1 Ln(CU) + d_2 (Ln(CU))^2 \tag{5}$$

where d_0, d_1, d_2 are the regression coefficients to be estimated.

2.4. *Calculating optimal chilling duration*

It follows from applying the first order condition for Eq. (1) that the optimal chilling duration (its logarithm) $Ln(CU^*)$ that provides the stem maximal length L^*, can be calculated using the following formula:

$$Ln(CU^*) = -b_1/(2b_2) \tag{6}$$

Applying the same condition for Eq. (5), the optimal chilling duration (its logarithm) $Ln(CU^*)$ that provides the maximal profit P^*, can be calculated using the following formula:

$$Ln(CU^*) = -d_1/(2d_2) \tag{7}$$

Each of the optima L^*, P^* are calculated using the models (1) and (5) for the corresponding values $Ln(CU^*)$ of chill units. The method of inverse confidence intervals can be used to calculate confidence intervals for these values of chill units (Appendix A).

2.5. *The dynamic model of a stem weekly length*

In this section we present a dynamic model (by weeks of a stem elongation period) of a stem length. Richards [20] suggested that sigmoid growth curves – the logistic curve and its generalizations – could be used for the empirical description of plant growth. Guak and Neilsen [21] used the four parameter logistic function for describing days to budbreak as a function of chamber temperature of fruit trees dormancy in British Columbia.

In our study, the following form of the four parameter logistic function was used for the dynamic model:

$$l_t = l_0 + (l_\infty - l_0)/(1 + \exp(\alpha + \beta t)) \tag{8}$$

where t is the duration of a stem elongation (measured as days after transfer of the plant to the greenhouse); l_t is a stem length, in cm; and the four parameters of the function are defined as follows: l_0 is the lower bound for l_t observed at the beginning of the stem elongation period, l_∞ is the upper bound for l_t, α and β – parameters that define time shift factor and growth rate, respectively.

For every plant, values of l_t have been measured weekly. The lower asymptote l_0 equals 0 in this model. The predicted maximal stem length L_{pred} from the model (2) of stem maximal length can be used as the upper asymptote l_∞. Another possibility is to use an average stem length measured in the last week of stem elongation, as an estimate of l_∞.

Besides the estimation of weekly stem lengths, the other important output of this model is the determination of the time point $T_{\max}$ of the maximal growth rate of the stem. As follows from the article of Richards [20], $T_{\max}$ can be calculated by the following formula:

$$T_{\max} = -\alpha/\beta \tag{9}$$

This gives useful information on the inflection point of the logistic function where the growth rate of peony stems is maximal. Our data enable comparing values of $T_{\max}$ between different constant chilling temperatures and for different duration of chilling.

2.6. *Estimating inverse confidence intervals and between treatments differences*

Estimation of the models enables to examine between treatment differences for the following outputs:

- The chilling duration that brings to the maximal stem length L^*.
- The difference between values of L^* for different treatments.
- The chilling duration that brings to the maximal profit P^* per stem, for an exploratory example based on Eq. (5), and the value of this maximal profit.

In every model, we check the possibility to estimate a confidence interval for the optimal chilling duration. The estimation procedure for such inverse intervals ("inverse" because they relate not to the response variables – stem length or profit – but to the exploratory variable of chill units) is detailed in Appendix A.

3. Results

The model (1) was estimated using Microsoft Excel Data Analysis computer programs. The optimal value of chill units CU (the optimal chilling duration) was estimated when the average maximal stem length L for every registered value of chill units (in other words, for every week of dormancy release) was used as a response variable (Appendix B). For treatments 7 and 8, the optimal values CU^* are very close to one another – the difference equals 1.4%, whereas the between treatment difference for the optimal stem length L^* is significant (based on the t test) – the difference equals 27% (Table 1).

Additional details of the estimation of Eq. (1) for all three treatments are presented in Fig. 2. For treatment 9, the use of the model (1) did not enable finding the optimal CU^*. The data of this treatment were not used in the following stages of the model. The dynamics of elongation (in particular, the optimal value of chill units) is similar between treatments 7 and 8 but the maximal stem length is different as it was presented in Table 1. The results shown in Table 1 and Fig. 2 complement each other.

The model (5) was run to estimate the optimal value of chill units CU when the profit P was used as a response variable. The data for the exploratory example of the use of this model are detailed in Appendix B. For treatments 7 and 8, the optimal values CU^* are very close one to each other – the difference is less than 0.5%, whereas the between treatment difference for the optimal P^* is significant (based on the t test) – the difference equals 52% (Table 2).

In Table 2, the 90% confidence intervals for CU^* are estimated using the method of inverse confidence interval (Appendix A). For optimal values of CU^* from model (1) for the maximal stem length in Table 1 the inverse confidence intervals cannot be estimated. Possible failures in estimating inverse confidence intervals are explained by high fluctuation of the data [22].

Table 1 – Optimal values of chill units and stem length in model (1).

Treatments	CU^* in hours		CU^*	L^* in cm	
	CU^*	$Ln(CU^*)$	In week	L^*	$Ln(L^*)$
A – treatment 7	1959	7.58	11.7	60	4.09
B – treatment 8	1987	7.59	11.8	47	3.85
A:B	98.6%	99.8%	98.6%	127.0%	106.2%

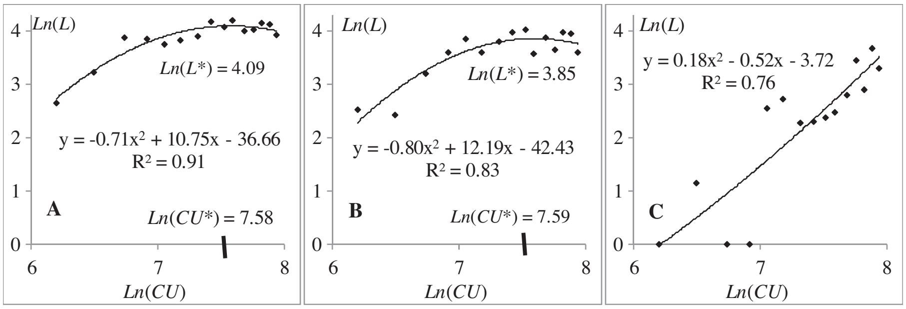

Fig. 2 – Maximal stem length fitted with Eq. (1). A – treatment 7, B – treatment 8, C – treatment 9 (compare with data shown in Table 1).

Table 2 – Optimal values of chill units and profit in model (5).

Treatments	CU^*, weeks	Inverse confidence intervals for CU^*		P^*, NIS
		Weeks	% of CU^*	
A – treatment 7	6.80	(5.9, 7.5)	(87%, 111%)	5.99
B – treatment 8	6.84	(5.2, 8.0)	(77%, 118%)	3.93
A:B	100%			152%

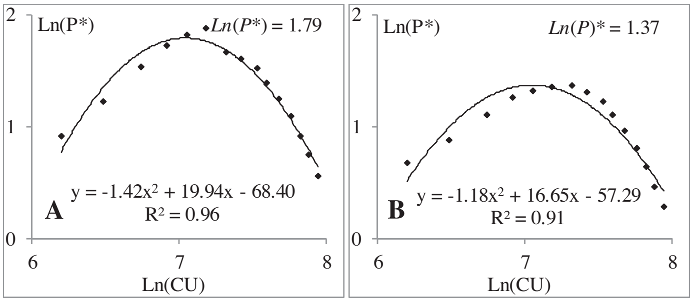

Fig. 3 – Profit maximisation under varying chilling duration using model (5). A – treatment 7, B – treatment 8 (compare with data shown in Table 2).

The results of the estimation of Eq. (5) are compared for treatments 7 and 8 in Fig. 3. In agreement with the results from Table 2, the dynamics of stem elongation is similar between treatments 7 and 8 but the maximal profit is different.

The time point T_{max} – a week in which the stem growth rate was maximal, decreases as duration of chilling increases. The decrease in T_{max} is approximately the same for both treatments 7 and 8 – from T_{max} equal 5–6 weeks for a short chilling duration of 4–5 weeks, down to T_{max} equal 3–4 weeks for a longer chilling duration of 15 and more weeks (Fig. 4).

The dynamic model (8) was estimated using Microsoft Excel Data Analysis and Solver programs. An example of a logistic growth function estimated for the plants from treatment 7 for which the chilling duration was 9 weeks, is shown in Fig. 5.

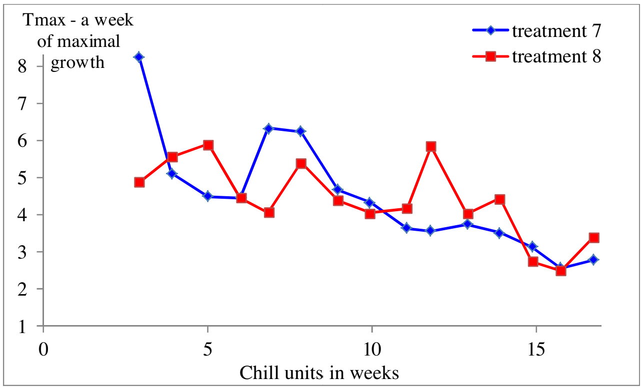

Fig. 4 – T_{max} for treatments 7 and 8 for various chilling duration.

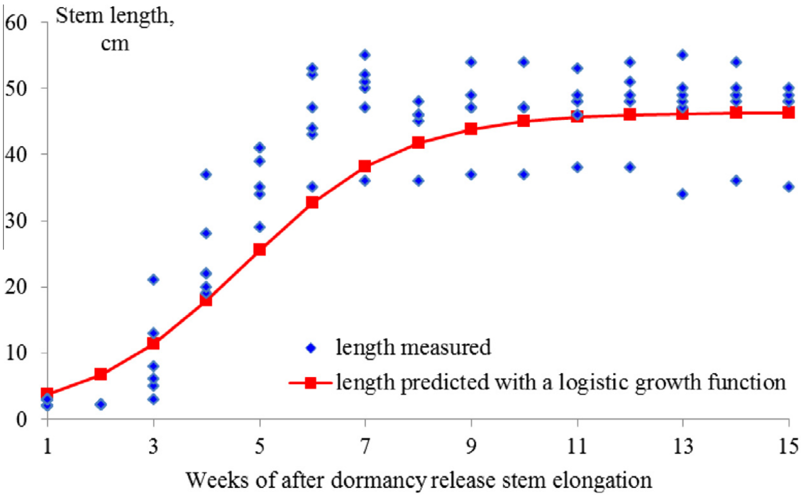

Fig. 5 – Stem elongation in treatment 7, for 9 weeks chilling duration – measured stem lengths and their prediction with a logistic growth function.

Table A.1 – Data for the estimation of the model (5) parameters.

Item	NIS
Fixed cost, per flower	0.10
Variable cost, per flower	0.127 in treatment 7, 0.108 in treatment 8 (15% less because of lower chilling temperature)
Benchmark price $Price_b$, per flower	0.50
$Price_{bonus}$ per cm, the stem length < 54 cm	0.042
$Price_{bonus}$ per cm, the stem length ⩾ 54 cm	0.038

4. Conclusion and discussion

In this study, the models of stem elongation responses to dormancy conditions of peony are developed. These models are based on the quadratic regression of stem length on chill units accumulated during the chilling period. We use the logarithms of the variables to reduce the effect of possible outliers. For the after dormancy release phase, a dynamic model of weekly stem elongation was developed based on the logistic growth function.

4.1. *Conclusion*

The results can be concluded as follows.

(1) The quadratic regression models perform well in treatments 7 and 8 with constant temperatures of 2 °C, 6 °C in cooling chambers but not in treatment 9 with a temperature of 10 °C.

(2) For treatments 7 and 8, the optimal values of chill units (in the models of a maximal stem length and maximal profit of farmers) are close to one another, and the values of a maximal stem length and maximal profit are significantly different. For the model of maximal profit, the inverse confidence intervals of chill units were successfully estimated.

(3) For both treatments 7 and 8, the week number T_{max} when the stem growth is maximal, decreases by approximately the same rate as duration of chilling increases: from weeks number 5–6 for short chilling duration to weeks number 3–4 for longer chilling duration.

(4) For every specific treatment and chilling duration, the logistic growth function (calculated by weeks of the after dormancy release period) can be estimated. We propose the method when the output of the quadratic regression model (of the maximal stem length) serves an input parameter (an upper asymptote) of the logistic function.

4.2. *Discussion*

Our findings are in line with other studies where quadratic functions for modelling stem elongation responses to dormancy conditions are used. In the study of Jones et al. [23] a number of empirical chilling models were tested to explain the interaction between chilling temperature and period, and bud development of blackcurrant cropping affected by warm winters. The best model involved a quadratic function of chilling time dependent on the temperature factor.

In the study of Bouwmeester and Karssen [24] the role of temperature in dormancy and germination changes in seeds of *Polygonum persicaria* was studied. In this study, a quadratic function describing germination in% after dormancy relief was used. For seeds exposed to the constant dormancy temperature of 2 °C the optimal result (germination,%) was achieved for approximately 10 weeks both for germination at 20 °C and 30 °C. For lower temperature of germination at 10 °C the optimal (but much less convincing) result was achieved for approximately 15 weeks (Fig. 4 B in the above-mentioned article). In our study, the large used database enabled modelling stem elongation responses to dormancy conditions and growth functions separately for every value of chilling duration – from 3 to 17 weeks.

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Appendix A

Calculation of the inverse confidence interval for the optimal chill units

From Eq. (1), the optimum value of the chill units is calculated as follows:

$$CU_{opt} = -b_1/(2b_2) \tag{10}$$

This value is a ratio of two regression coefficients. Therefore its variance and confidence limits can be calculated in terms of variances of the regression variables and residuals. The confidence limits of CU_{opt} are called the “inverse” confidence limits because they relate to the exploratory variable CU. These limits CU_L (the lower limit) and CU_U (the upper one) can be calculated as follows:

$$CU_L, CU_U = CU_{opt}\left(1 - g_{12} \pm \sqrt{(1-g_{12})^2 - (1-g_{11})(1-g_{22})}\right)/(1-g_{22}) \tag{11}$$

where the signs minus and plus refer to the lower and the upper limits, respectively.

The symbol g_{hi} is defined as $g_{hi} = t^2 s^2 t^{hi}/(b_h b_i)$ where t – the value of the t-statistic corresponding to n-3 degrees of freedom (n is the sample size) and a selected level of significance, s^2 – the residual mean square, b_h, b_i – the regression coefficients (h, i = 1, 2, 3), t^{hi} – the elements of the inverse of the variance–covariance matrix of the regression coefficients [22,25].

Appendix B

Data for estimation of model (5) parameters

For every six plants that were transformed weekly from the chilling chambers to the greenhouse, their average maximal sprout length L was calculated, in cm. For every treatment, the plants were transferred to the greenhouse every week for 15 weeks.

The data used for the exploratory example of estimating the model of the quadratic regression of farmers’ profit on chill units are shown in Table A.1. For the assumptions shown in Table A.1, Israeli farmers’ data were used.

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