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A MODEL OF LEAF GROWTH RESPONDING TO AIR TEMPERATURES

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CHIKUSHI J. and EGUCHI H. *A model of leaf growth responding to air temperatures.* BIOTRONICS **20**, 65–71, 1991. A hysteresis model was applied to estimate leaf growth curve of cucumber leaf exposed to changing air temperature. Cucumber plants were treated with low temperature of 15℃ for different periods, and thereafter grown at 25℃ in a growth chamber. Observed data of leaf growth curves were fitted by the Richards equation, and were compared with the curves estimated by the model. It was demonstrated that the hysteresis model can be useful for estimating the curves of leaf growth responding to the low temperature treatment.

Key words: *Cucumis sativus* L.; cucumber; leaf growth; air temperature; Richards equation; non-linear optimization; Powell method; hysteresis model.

INTRODUCTION

Plant growth depends on air temperature (*3, 5, 9, 12, 18*), and the relation between the growth and the temperature has been analyzed by using the monomolecular, the Gomperz, the logistic and the Richards equations. These equations can be useful for fitting curves for observed data. Furthermore, it is essential to develop more reliable equation for predicting plant growth responses to dynamic environmental factors.

The present paper deals with the examination of a proposed equation derived from hysteresis model, for estimating growth curves of leaves exposed to low air temperatures.

MATERIALS AND METHODS

Plant materials

Cucumber plants (*Cucumis sativus* L. var. Hot. Chojitsu-Ochiai) were precultured at air temperature of 20℃, relative humidity of 70%, and light intensity of 250 μmol m^{-2} s^{-1} in photoperiod of 12 h. At the first leaf stage, plants were treated with a low temperature of 15℃ for respective periods of 0, 9, 11 days and continuous treatment in a growth chamber. Time was set as 0 d at the commencement of the low temperature treatment. After each period of the low temperature treatment, air temperature was changed to 25℃. The third leaf was used as a specimen and photographed at an interval of 24 h. Position data were read with a digitizer (KD4030A, Graphtec Corp.) along the perimeter of the leaf. Leaf area was calculated from these data by numerical analysis.

Curve fitting

In general, the Richards equation (*16*) is useful for expressing the time course of plant growth (*1, 6*). The following Richards equation modified with a little correction, was used for the curve fitting.

$$S(t)=\frac{S_o S_f}{\{S_o{}^n+(S_f{}^n-S_o{}^n)e^{-k(t-m)}\}^{1/n}} \tag{1}$$

where $S(t)$, a leaf area at time t; S_o, a predicted initial leaf area (S at $t=m$); S_f, asymptotic or final leaf area (S at $t\to\infty$); and k, m and n, constant. In Eq. (1), n is in a range of $-1\leqq n<\infty$ without $n=0$, and t in the original Richards equation was replaced by $t-m$ to avoid $S_o<0$, in which case calculation of $S_o{}^n$ is impossible during the searching operation of the parameters. Equation (1) is expressed as the monomolecular equation when $n=-1$ and as the logistic equation when $n=1$, and this approaches to the Gomperz equation in form as n approaches to zero (*8*). There are five parameters of S_f, S_o, k, m and n in Eq. (1). Richards (*16*) have obtained the parameters by using an empirical method of fitting, which is not only very laborious but can produce misleading results (*2*). It is more efficient to employ the non-linear least square method to determine these parameters. The residual sum of square with reference to S can be used as an objective function as expressed by

$$F=\sum_{i=1}^{N}(S_i-S_{oi})^2 \tag{2}$$

where S_i is substituted with $S(t)$ in Eq. (1); S_{oi}, observed data; N, the number of data. There are several methods for minimizing the objective function F (Eq. 2). Nelder (*14*) and Causton (*2*) have introduced the Newton method for determining the parameters, and Davies and Ku (*4*) criticized it for giving misleading results. In the present study, the Powell method was used for rapid convergence (*11*). In this method, the algorithm for searching a minimum value of F is based on the conjugate direction method; linearly independent directions for the searching, which are chosen to be the coordinate directions initially, are modified to become conjugate directions during the iteration process of the searching. This method have an advantage that it needs no explicit evaluation of derivatives. When the searching directions are not linearly independent, the convergence of solution can not be assured. In consideration of this point, Kanoh (*11*) has summarized the method modified by Zangwill (*17*).

Curve-estimating model

A model for scanning curves in hysteresis phenomena was applied to the estimation of growth curves with the low temperature treatment on the basis of similarity between hysteresis curves and growth curves. Hysteresis phenomena can be encountered in the relationships between magnetic field strength and intensity of magnetization, between stress and strain, between soil water content and suction, *etc.* (*7, 10*). Each relationship causes, in many cases, a hysteresis loop composed of different boundary curves. Within the loop, countless scanning curves could be considered ; a value of one variable depends on changing process of another variable (*i.e.*, increasing or decreasing process). For the estimation of growth curves, the conceptual model developed by Mualem (*13*) could be useful because of the suitable determination of scanning curves by only two boundary curves. The model equation (*13*) is

$$S(t)=S_d(t)+\frac{\{S_d(t_1)-S_d(t)\}\{S_a(t)-S_d(t)\}}{S_u-S_d(t)} \tag{3}$$

where t, time ; S_a and S_d, respective leaf areas in boundary curves of A and D in Fig. 1 ; $S(t)$, leaf area at time t after the low temperature treatment with 15℃ up to time t_1 ; S_u was treated as zero.

RESULTS AND DISCUSSION

Figure 1 shows the time courses of leaf area under different conditions of the low temperature treatment. In the figure, A-, B-, C-, and D-curves correspond to non-treatment (*i.e.*, plants were grown continuously under air temperature of

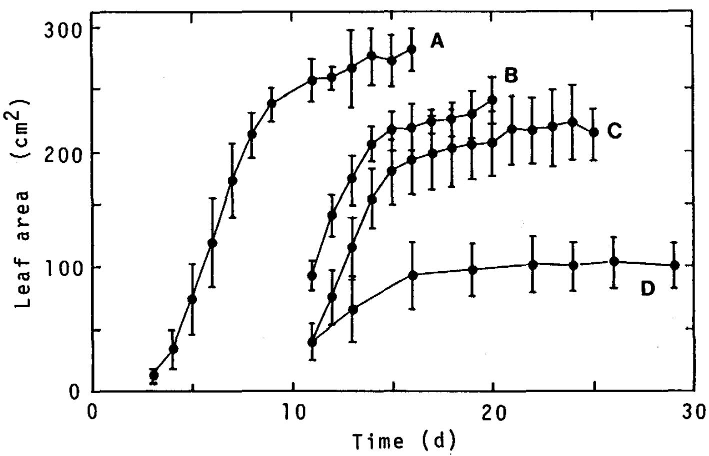

Fig. 1. Experimental leaf growth curves of cucumber plant for different periods of the low temperature treatments ; 0 day (A), 9 days (B), 11 days (C), and continuous (D) treatments. Bars indicate 95% confidence intervals.

25℃), 9 days treatment, 11 days treatment, and continuous treatment (*i.e.*, plants were grown continuously under air temperature of 15℃), respectively. In A-curve, leaf area rapidly increased with time, asymptotic value of leaf area became high and growth duration was short. On the other hand, in D-curve, asymptotic value of leaf area became low and growth duration was long. B- and C-curves were found to be intermediate growth patterns between A- and D-curves. From these results, it is indicated that growth rate deteriorates with the period of the low temperature treatment.

Figure 2 shows a comparison between observed values and fitted curves. In A-curve, five parameters in Eq. (1) were determined, while in D-curve, three parameters were determined because leaf area was assumed as a low value (0.01 cm^2) at $t=0$. B- and C-curves were fitted to pass through the points on the D-curve at time of 9 and 11 days, respectively. Agreement of these curves with observed data demonstrated that the Richards equation can be reliably used as a fitting equation for various growth curves as described by Cao *et al.* (*1*) and Dennett *et al.* (*6*). By using A- and D-curves, which were assumed as boundary curves in hysteresis loop, we estimated growth curves of B and C corresponding to the low temperature treatments for 9 and 11 days, respectively. Results of the estimation were shown in Fig. 3 with observed values. Estimation of the curves was very fine.

Figure 4 shows a group of estimated growth curves with the period of the low temperature treatment; here the period was taken with two days increment. From the results, it is feasible to understand aspect of leaf growth responding to the low temperature treatment: Delayed leaf growth was found during the low temperature treatment and thereafter the growth rapidly rose. Asymptotic values decreased with longer periods of the low temperature treatment. Figure 5 shows the variation of asymptotic value as a function of period of the low

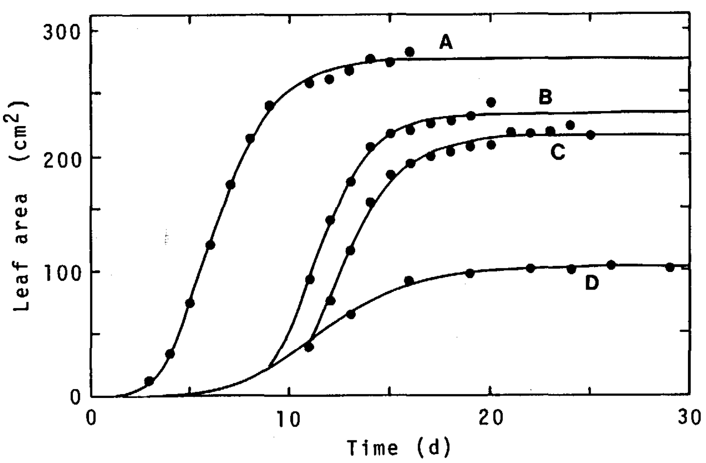

Fig. 2. Curve fitting of leaf growth data by using the Richards equation for four different periods of the low temperature treatments; 0 day (A), 9 days (B), 11 days (C), and continuous (D) treatments.

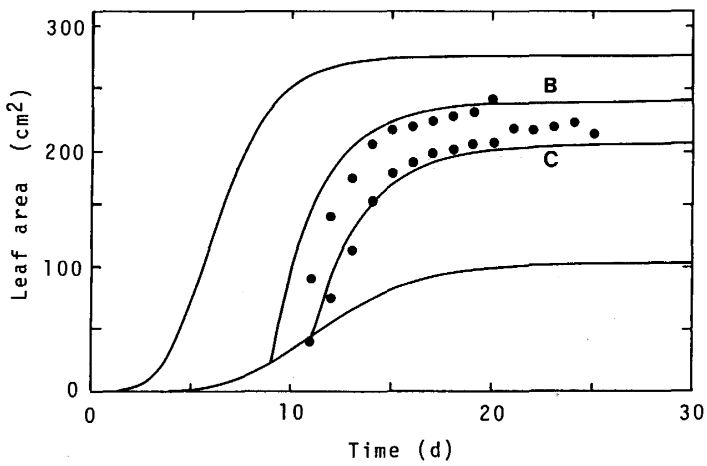

Fig. 3. Comparison of leaf growth data (black circle) with estimated curves by hysteresis model (solid line) for 9 days (B) and 11 days (C) low temperature treatments.

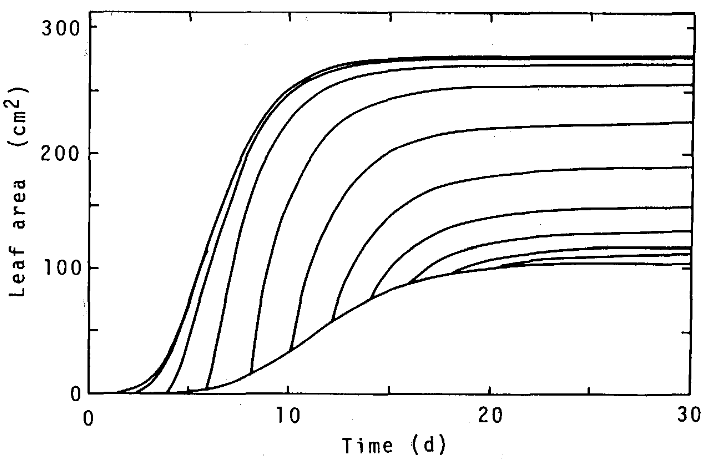

Fig. 4. Simulation of leaf growth curve for different periods of the low temperature treatments.

temperature treatment. Two plotted data in Fig. 5 indicate the asymptotic values of B- and C-curves obtained from the fitting by using Eq. (1). The estimated curve of asymptotic leaf area coincided with these two values. The prediction of asymptotic leaf area has been mentioned to be difficult (*15*), because of dependence on both the duration of growth and the mean of weighted growth rate, and other stresses. From the present experiments, it was found, however, that when two different growth curves (boundary curves) are determined, every growth curve can be predicted within a region between the two curves by using the hysteresis model.

Thus, it was clarified that the conceptual model of Eq. (3) in hysteresis

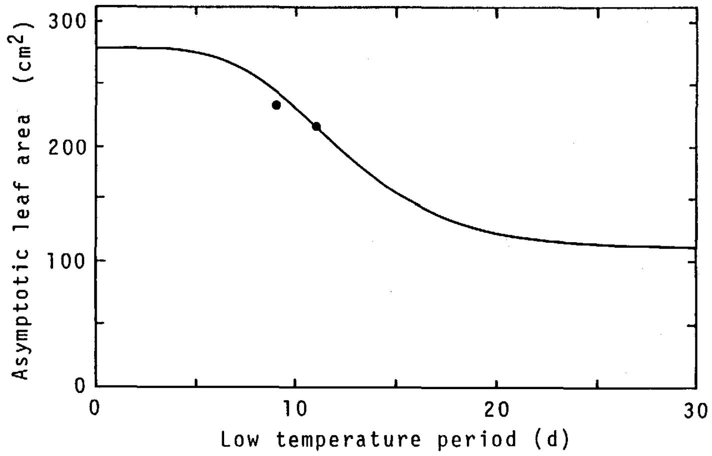

Fig. 5. Relationship between asymptotic leaf area and period of the low temperature treatments.

developed by Mualem can be effective to estimate the curves of leaf growth exposed to changing air temperature.

REFERENCES

1. Cao J., Hesketh J. D., Zur B. and Reid J. F. (1988) Leaf area development in maize and soybean plants. *Biotronics* **17,** 9–15.
2. Causton D. R. (1969) A computer program for fitting the Richards function. *Biometrics* **25,** 401–409.
3. Causton D. R., Elias C. O. and Hadley P. (1978) Biometrical studies of plant growth. 1. The Richards function, and its application in analysing the effects of temperature on leaf growth. *Plant, Cell and Environ.* **1,** 163–184.
4. Davies D. L. and Ku J. Y. (1972) Re-examination of the fitting the Richards growth function. *Biometrics* **33** 546–547.
5. Dennett M. D. and Auld B. A. (1980) The effects of position and temperature on the expansion of leaves of *Vicia faba* L. *Ann. Bot.* **46,** 511–517.
6. Dennett M. D. Auld B. A, and Elston J. C. (1978) A description of leaf growth in *Vicia faba* L. *Ann. Bot.* **42,** 223–232.
7. Everett D. H. and Whitton W. I. (1952) A general approach to hysteresis. *Trans. Farady Soc.* **48,** 749–757.
8. France J. and Thornley J. H. M. (1984) *Mathematical Models in Agriculture, A Quantitative Approach to Problems in Agriculture and Related Sciences.* Pages 75–94, Butterworth & Co., Ltd., London.
9. Friend D. J. C., Helson V. A. and Fisher J. E. (1965) Change in the leaf area ratio during growth of marquis wheat, as affected by temperature and light intensity. *Can. J. Bot.* **43,** 15–28.
10. Hillel D. (1980) *Fundamentals of Soil Physics.* Pages. 152–155, Academic Press, New York.
11. Kanoh H. (1987) *Theory and Computational Methods in Optimization* (*Sisutemu no Saitekiron to Saitekika*). Pages 82–84, Corona Publishing Co., Ltd., Tokyo (in Japanese).
12. Milford F. J., Pocock T. O. and Riley J. (1985) An analysis of leaf growth in sugar beat. 1. Leaf appearance and expansion in relation to temperature under controlled

conditions. *Ann. appl. Biol.* **106,** 163–172.
13. Mualem Y. (1974) A conceptual model of hysteresis. *Water Resour. Res.* **10,** 514–520.
14. Nelder J. A. (1961) The fitting of the logistic curve. *Biometrics* **17,** 89–110.
15. Reid J. F., Zur B. and Hesketh J. D. (1990) The dynamics of a maize canopy development. 2. Leaf area growth. *Biotronics* **19,** 99–107.
16. Richards F. J. (1959) A flexible growth function for empirical use. *J. exp. Bot.* **10,** 290–300.
17. Zangwill H. (1967) Minimizing a function without calculating derivatives. *Computer J.* **10,** 293–296.
18. Zur B., Reid J. F. and Hesketh J. D. (1989) The dynamics of a maize canopy development. 1. Leaf ontogeny. *Biotronics* **18,** 55–66.