

Modeling the Interactive Effect of the Photoperiod and Temperature on Shoot Elongation of Mulberry

Kuniaki Fukui

(National Institute of Agrobiological Sciences, Ohwashi 1-2, Tsukuba, Ibaraki 305-8634, Japan)

Abstract : Potted mulberry plants (*Morus alba* L. 'Shinn-ichinose') were grown in phytotrons under natural sunlight, and their shoot growth response to temperature and photoperiod was investigated. A short photoperiod caused cessation of shoot growth, and this effect was prominent at 20°C. Temperatures higher than 24°C activated the growth activity for mulberry shoot growth. Temperature had two effects on mulberry shoot elongation. One was to control the growth activity of mulberry shoots, and the other was to determine the potential rate of shoot elongation, which is realized at the maximum growth activity under a given environmental condition. On the basis of these results, the effect of temperature and photoperiod on the cessation of mulberry shoot elongation was simulated in a non-linear regression model. The values of shoot length predicted by the model differed somewhat from the measured values in some plots, most likely because the timing of shoot growth cessation differed with the year. However, on the whole, shoot length predicted by the model seems to fit the measured values well.

Key words : Model, Mulberry, Phenology, Photoperiod, Shoot length, Temperature, Temperature and photoperiod interaction, Tree.

Mulberry (*Morus alba* L.) is a tree crop which is used for rearing silkworms. Since the tree's assimilatory organs are harvested during vegetative growth, and since removing them is a heavy stress for the mulberry tree, it is important to evaluate and predict the state of growth in order to obtain a stable yield. Simulation models have been developed for many crops, and are used for crop management (Hanks and Ritchie, 1991). However, there is no model to predict the vegetative growth of mulberry, although Ito (1991) constructed a prediction model for spring sprouting time. Thus, I endeavored to investigate the relationship between mulberry growth and environmental factors, and to develop a simulation model for mulberry vegetative growth. Ultimately, I intend to use the model for mulberry cultivation management.

Previously (Fukui, 2000), I investigated the relationship between mulberry growth and temperature, and constructed a model of shoot elongation. However, photoperiod plays an important role in growth cessation in trees and, this factor was not considered in that model. Howe et al. (1995) suggested that growth cessation of black cottonwood was controlled by photoperiodic sensitivity and the longest photoperiod that elicited a short-day response. Junttila (1982) showed that there were ecotypical differences in photoperiodic growth cessation in *Salix*. Photoperiod-induced phenological responses are incorporated in growth models for many other crops, such as rice (Horie and Nakagawa, 1990), wheat (Ritchie, 1991) and maize (Kiniry, 1991). Thus,

in order to precisely predict mulberry growth, it is necessary to incorporate the effects of photoperiod on phenology in a mulberry growth model.

Yan and Wallance (1998) emphasized the effect of temperature and photoperiod interaction on plant phenology, and incorporated the interaction effect in their plant phenological model. Some authors have reported the effect of this interaction on the phenology of trees. Heide (1974) reported that temperature significantly modified the effects of photoperiod, but only slightly changed the critical photoperiod for growth cessation in Norway spruce. Junttila (1980) showed the interaction effects on apical growth cessation in willow and birch. There is, however, no information about how temperature and photoperiod control cessation of mulberry growth, although Hamada (1933) and Taguchi and Kikuchi (1951) reported that a short photoperiod depressed mulberry growth. Therefore, an investigation of the effect of the interaction between temperature and photoperiod on mulberry growth and growth cessation would be desirable.

In this study, I investigated the growth response of mulberry to photoperiod and temperature in a controlled environment under natural sunlight. From the data, I evaluated the effects of temperature and photoperiod on mulberry shoot growth, and constructed a simulation model of mulberry shoot elongation.

Table 1. Dates of the start and the end of treatment in each plot, and temperature and photoperiod during the experimental period in each group.

Plot	Beginning	End	Temperature (°C)	Photoperiod (hour)
1	20 Aug. 1998	9 Nov. 1998	27, 20	13.3-10.4
2	27 May. 1999	30 Jul. 1999	27, 19	14.3-14.6-14.0
3	13 Aug. 1999	8 Nov. 1999	30, 24	13.6-10.4
4	27 May. 1999	27 Jul. 2000	28, 20	14.3-14.6-14.1
5	5 Aug. 2000	6 Nov. 2000	28, 20	13.8-10.5
6	27 May. 1999	13 Jul. 2001	28, 24	14.2-14.6-14.4
7	24 Aug. 2001	5 Nov. 2001	28, 24	13.2-10.5
8	26 Dec. 1999	24 Mar. 2000	28, 20	14.0
9	23 Jan. 2000	24 Mar. 2000	28, 20	14.0

Materials and Methods

Mulberry plants (cv. Shinn-ichinose) were placed individually in pots with a surface area of 0.05 m² (30cm high and 50.4 cm in diameter) in 1996. There were 9 experiments, each consisting of two groups; each group of plants was grown in a phytotron at a constant temperature under natural sunlight (Table 1). The actual air temperature in the phytotrons fluctuated about the desired temperature (Table 1) within a range of $\pm 5.0^{\circ}\text{C}$. The plants were fertilized once every two weeks with 2.0 g N, 0.8 g P₂O₅, and 0.8 g K. Each pot was watered moderately by an automatic drip irrigation system during the treatments. A systemic insecticide was applied to each pot at the beginning of the treatment.

In experimental plots 1 through 7, each pot had one shoot, and the shoot length ranged from 50 to 180 cm at the start of the treatment. Mulberry plants in plots 2, 4, and 6 sprouted in April, after winter dormancy. Mulberry plants in plots 1, 3, 5 and 7 were cut back in early June and sprouted in June. Sixty plants were prepared for each plot, and half of them were used for each temperature treatment. In experimental plot 8 and 9, eleven mulberry plants were moved into each phytotron before shoot sprouting. After all of the mulberry plants sprouted in each phytotron, I pruned the plants so that they each had a uniform shoot. Two fluorescent lamps were lit from 5 : 00 to 7 : 00 and from 17 : 00 to 19 : 00 to provide a constant photoperiod of 14 hours in plots 8 and 9.

Shoot length was measured once or twice a week, and the state of the growing point was checked each time. The state of the shoot apex was defined as follows. In the active state, there are several small new leaves around the shoot tip, and the mulberry plant is growing normally. In the inactive state, only one or two small leaves surround the shoot tip, and mulberry growth has lost its vigor. In the quiescent state, there are no new leaves around the shoot tip, and the mulberry plant has stopped growth.

Results and Discussion

1. Experimental results

Figs. 1A and B illustrate the changes in shoot length which took place with each temperature treatment. Shoot length became longer as the temperature increased, similar to the results of Fukui (2000). In plots 1, 3 and 5 which were treated after August (Table 1), the elongation rate became slower with time. Fig. 1C shows the changes in shoot elongation rates in plots 4 and 5 in 2000, and in 6 and 7 in 2001. At 24 and 28°C, there was little difference between the elongation rates in the plots treated from May (4 and 6) and from August (5 and 7) in both years. However, at 20°C, the elongation rate in the plot treated from August (5) dropped more markedly than that in the plot treated from May (4). Fig. 2 shows the changes in the state of the shoot apices at 28, 24 and 20°C examined in 2000 and 2001. The activity of the shoot apex in the plots treated from August was inferior to that in the plots treated from May, even at 24 and 28 °C. Downs and Borthwick (1956) showed that shoot growth was prevented by a short photoperiod in many tree species, and Taguchi and Kikuchi (1951) showed that mulberry growth was also suppressed by a short photoperiod. Growth was not inferior in the prolonged photoperiod conditions applied in plots 8 and 9 (Fig. 1D). Therefore, the decrease in the elongation rate and the poor activity of the shoot apex in the plots treated from August (5 and 7) seems to be caused by the short photoperiod. These results suggest that a low temperature intensified the growth suppression by a short photoperiods, although negative effects of short photoperiods on growth can be found at all temperatures. On the other hand, Heide (1974) showed that growth cessation caused by a short photoperiod was hastened by exposure to a higher temperature in Norway spruce seedlings. Junttila (1980) observed the same phenomena in the growth of willow and birch seedlings. Yan and Wallance (1996) considered the interaction of photoperiod and temperature, and they suggested that a photoperiod gene becomes active at higher temperatures. These

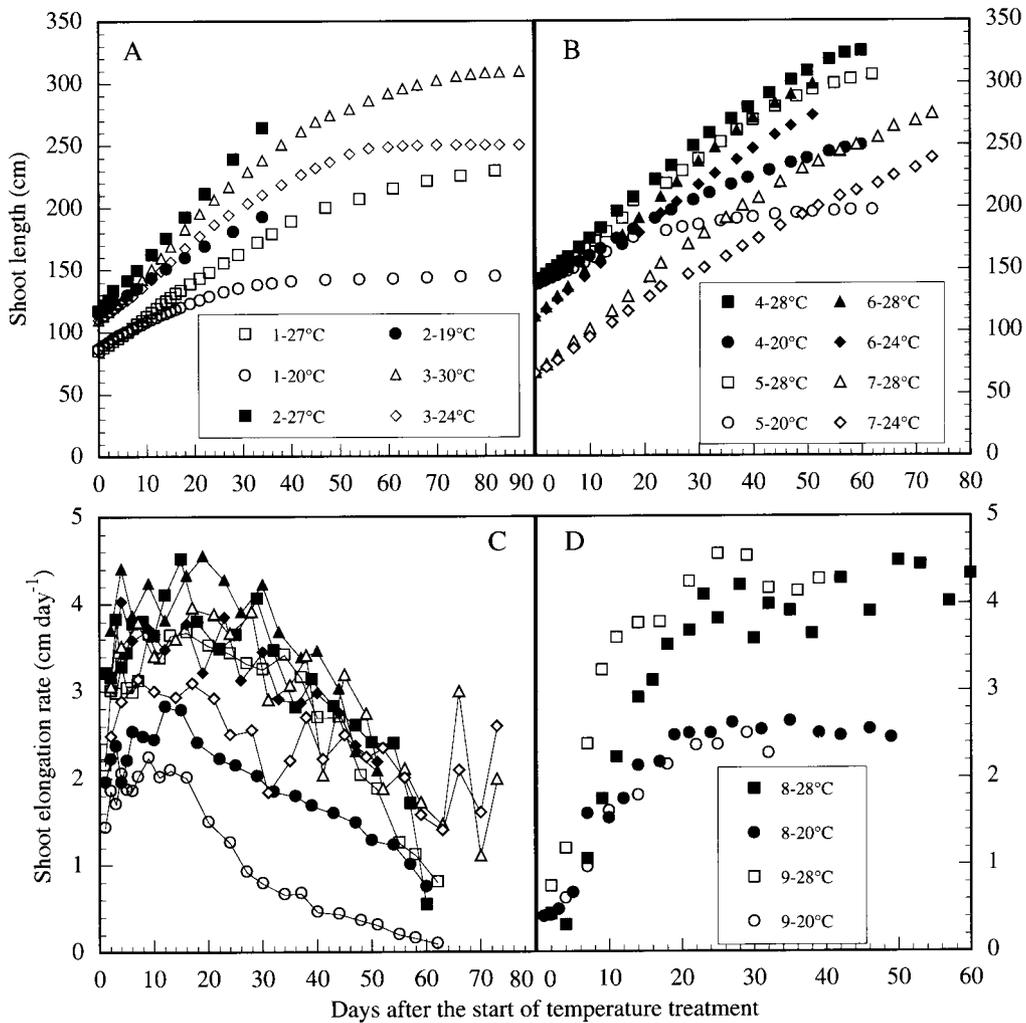


Fig. 1. Shoot length (A and B) and shoot elongation rate (C and D) during the temperature treatments. The symbols in C are the same as in B.

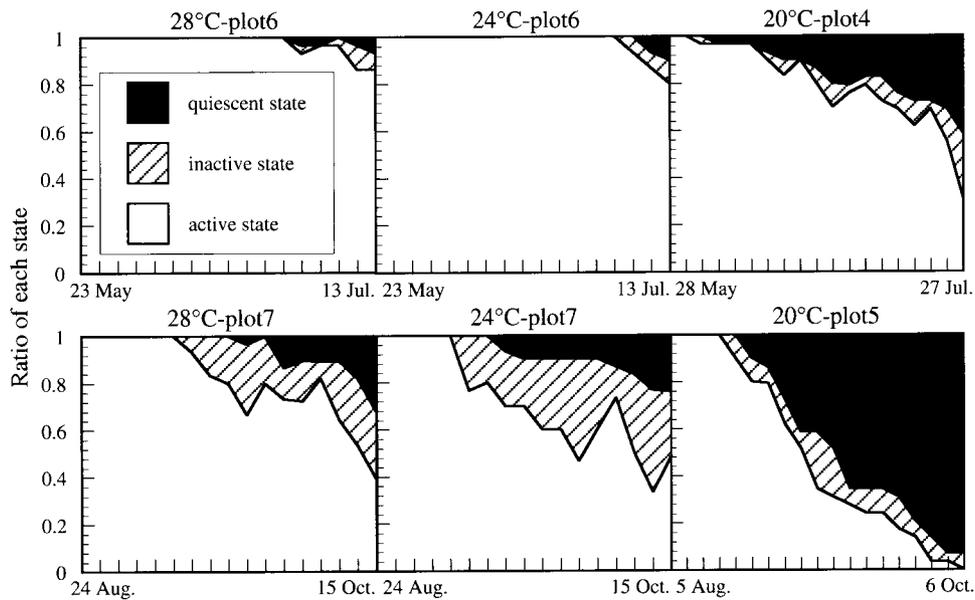


Fig. 2. Changes in the state of the shoot apex in the plants grown at 20, 24 and 28°C.

findings are the opposite of the results in the present research. To clarify the difference, I considered the growth behavior of individual mulberry plants in this study.

Since Fig. 1 merely shows the average values of shoot length and shoot elongation rate, there is no information about the growth behavior of individual potted mulberry plants. Interesting growth responses were found in individual potted mulberry plants grown at temperatures above 24°C in the plots of experiments 1, 3, 5 and 7. Fig.3 shows an example of the changes in shoot elongation rate in two individual potted mulberries. It seems that the growth of these mulberries slowed down gradually, exhibiting a wave shape in the graph. The wave-shaped graph line resulted from rapid growth depression, followed by growth acceleration, and was usually accompanied by color change in the shoot tip. When the shoot elongation rate slowed down, the shoot tip turned yellow, and when the rate recovered, the color returned to green. The mulberries which had this cycle of growth cessation and resumption usually showed it once or twice during the temperature treatment. There are many such mulberry plants in the treatments at a temperature higher than 24°C; however, only a few plants at 20°C. The cycle of growth depression and activation occurred on mulberry plants irrespective of shoot height. Junttila (1976) showed that *Salix* stem apices stopped growing in a short photoperiod, and resumed growth in a long photoperiod. In the present study, it seems that a short photoperiod had a suppressive effect on mulberry growth, and that a higher temperature activated the shoot apex. Such opposite effects of short photoperiod and high temperature on the shoot growth might have caused the cycle. In 2000, I transported two mulberry plants, which had stopped growing at 20°C, to the 28°C temperature condition after the end of the experiment. One plant showed no response, but the other mulberry resumed growth 14 days after the move. From this result, it seems that the daily average temperature for some period of time determines whether or not activity of the mulberry growth point is promoted, and that a high temperature has an activating effect on the shoot apex. Therefore, the promotive effect of a high temperature on the activity of the shoot apex may hide a high temperature effect on the photoperiod gene which suppresses the shoot growth, and thus, the results in the present experiment would be the opposite of previous reports.

2. Modeling

Fukui (2000) constructed a simulation model of mulberry shoot growth based on temperature and degree of mulberry development. Further in this investigation, I constructed a mulberry growth model based on temperature and photoperiod, using

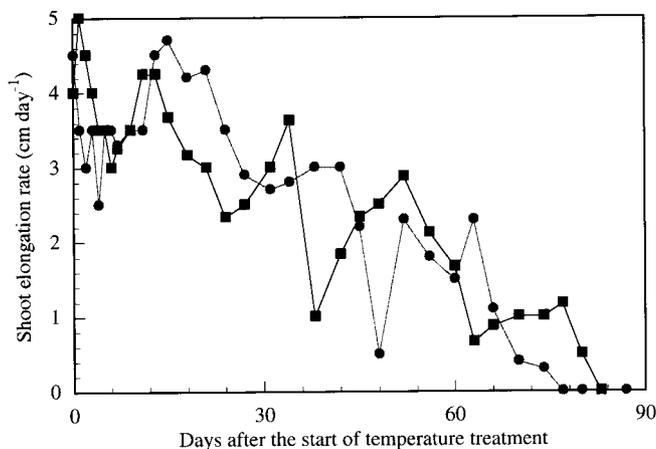


Fig. 3. Two examples of the change in shoot elongation rate of individual potted mulberries.

the data of plots 1, 3, 5 and 7. I did not consider the phasic difference in responses to temperature and photoperiod in order to simplify the model, because shoot length in many mulberry plants in my experiments was more than 100cm, while Fukui (2000) showed that the elongation rate increased with growth until a shoot length of about 100 cm, and then the rate became more or less constant. Other factors, such as water and nutrients, are presumed to be sufficient for plant growth. Since the ultimate object of this study was to predict the average shoot growth of mulberries in field conditions, I constructed a model of growth based on a group of plants, not on that of individual plants.

The mulberry shoot length model constructed here follows the design of Fukui (2000). Shoot length, S , is determined by :

$$S(x) = S(x-1) + s \quad (1)$$

Where $S(x)$ is shoot length (cm) at the x th day from the commencement of the treatment, and s is the daily shoot elongation (cm day^{-1}). The first measured values of shoot length were used as the initial values. Daily shoot elongation (cm day^{-1}), s , was presumed to depend on temperature and photoperiod.

Tollenaar et al. (1979) applied a cubic function to express the relationship between temperature and the rate of leaf appearance in maize, and Jones et al. (1991) used a linear function for the relationship between temperature and vegetative development rate in soybeans. However, growth behavior of individual mulberry plants showed that both temperature and photoperiod control the growth activity of mulberry shoot and this behavior must be represented in the model, especially, in declining growth phase. Therefore, it is necessary to introduce a new concept to simulate growth decline. According to Fig. 2, a short photoperiod and low temperature suppressed the activity of mulberry shoot apex, and a high

temperature promoted it. I represent the growth activity (GA) as a function of environmental factors and introduced it to equation (1). I define GA as follows; GA represents growth activity of mulberry shoot apex by a dimensionless value ranging from 0 to 1. If GA is maximal, mulberry plants achieve the greatest growth under a given environmental condition, whereas if GA is minimal, the plants cannot grow under any condition. GA changes from the value of previous day. According to the experimental results, GA is suppressed by a low temperature and short photoperiod, and activated by a high temperature. The daily shoot elongation s in equation (1) is defined as,

$$s = PR \cdot GA \quad (2)$$

where PR (potential rate) is defined as the potential rate of shoot elongation realized at the maximum GA under a given environmental condition. PR is a function of temperature, because Fukui (2000) showed that the rate of mulberry shoot elongation increases with increasing temperature in the range of 15°C to 27°C, and becomes constant from 27°C to 31°C. How does photoperiod factor in? It seems that photoperiod has no effect on PR of shoot growth rate in seedlings of *Salix* (Junttila, 1980) and in saplings of northern ecotype of black cottonwood (Howe et al., 1995) but that PR of shoot growth depends on the photoperiod in the saplings of southern ecotype of black cottonwood (Howe et al., 1995). Thus, the effect of photoperiod varies with the species or ecotype. The data from this experiment (Fig. 1C) showed that the shoot elongation rate was slightly higher in the long photoperiod (plots 4 and 6) than in a short photoperiod (plots 5 and 7). However, the shoot elongation rate did not increase with the increase in photoperiod in plots 4 and 6. Since the effect of photoperiod on PR is not clear, I presumed that photoperiod has no effect on PR to simplify the model. I suppose that factors other than temperature and photoperiod had no effect on s in this experiment because nutrients, water and pesticide were applied sufficiently. I defined PR and GA as :

$$PR = PR_{\max} \cdot f_1(T) \quad (3)$$

$$GA(x) = GA(x-1) \cdot f_2(\text{Tave}) \cdot g(L) \quad (4)$$

where PR_{\max} is the maximum rate of shoot elongation; T is the daily average temperature; L is the daily photoperiod; and Tave is the average temperature for certain days. Functions, $f_1(T)$, $f_2(\text{Tave})$ and $g(L)$ are represented by equation (5), (6) and (7), respectively, which are described later. It is impossible from the data to decide how long growth temperature needs the period to affect the growth activity of mulberry shoot. However, the mulberry plants in this experiment were at the same temperature for the entire experimental period. Therefore, the length of the period did not need to be considered, and I chose the average

Table 2. Values of parameters in the non-linear regression model.

Parameters	
a_1	0.3312
a_2	0.2227
a_3	0.0144
$b_1(^{\circ}\text{C})$	4.7801
$b_2(^{\circ}\text{C})$	17.9794
$PR_{\max}(\text{cm day}^{-1})$	3.9252
Standard error (cm)	13.6016

temperature during the experimental period for Tave. According to the previous report (Fukui, 2000), $f_1(T)$ is supposed to be a sigmoid function. The shapes of the curves of $f_2(\text{Tave})$ and $g(L)$ are not apparent. It is difficult to investigate the shapes, because of difficulty in separating PR and GA. However, it is apparent from the current experimental results that there is a critical temperature or photoperiod below which GA decreases. I presume that $f_2(\text{Tave})$ and $g(L)$ are linear below critical values, since shoot elongation rate of mulberry increased linearly with increasing temperature up to the critical point (Fukui, 2000), and the shoot growth rate of *Salix* also increased linearly with increasing temperature (Junttila, 1982) and Summerfield et al. (1991) used a lineary relationship between the rate of crop development and photoperiod in their crop developmental models. $f_2(\text{Tave})$ effectively increases GA of individual mulberry plants and it is not clear whether $g(L)$ has a positive effect on GA or not. However, there seems to be no positive effect of $f_2(\text{Tave})$ and $g(L)$ on GA for average growth in the various treatments (Fig. 1C). Therefore, I defined $f_2(\text{Tave})$ and $g(L)$ above the critical values as 1 and the functions $f_2(\text{Tave})$ and $g(L)$ range from 0 to 1. I chose a sigmoid function for $f_2(\text{Tave})$. Based on the experimental data, the threshold of L in $g(L)$ was placed at 13 hours, since mulberry showed symptoms of growth depression in late August, when the photoperiod is about 13 hours at the Institute. I chose a linear function for $g(L)$. The functions $f_1(T)$, $f_2(\text{Tave})$ and $g(L)$ are :

$$f_1(T) = 1 / (1 + \exp(-a_1 \cdot (T - b_1))) \quad (5)$$

$$f_2(\text{Tave}) = 1 / (1 + \exp(-a_2 \cdot (\text{Tave} - b_2))) \quad (6)$$

$$g(L) = a_3 \cdot (L - 13) + 1 \quad (7)$$

where a_1 , a_2 , a_3 , b_1 and b_2 are parameters. When L becomes greater than 13, $g(L)$ is 1. The parameters in equations (5), (6) and (7) were estimated non-linearly by an iterative method, using the data of plot1, 3, 5 and 7. Table 2 shows the estimated parameters. The shoot length predicted by the model was compared with measured values in Fig. 4. The predicted values of shoot length from the start to the middle of the treatment were almost the same as the measured values except for plot1-27°C. Since GA has a little effect on shoot elongation rate in this period, the equation (5)

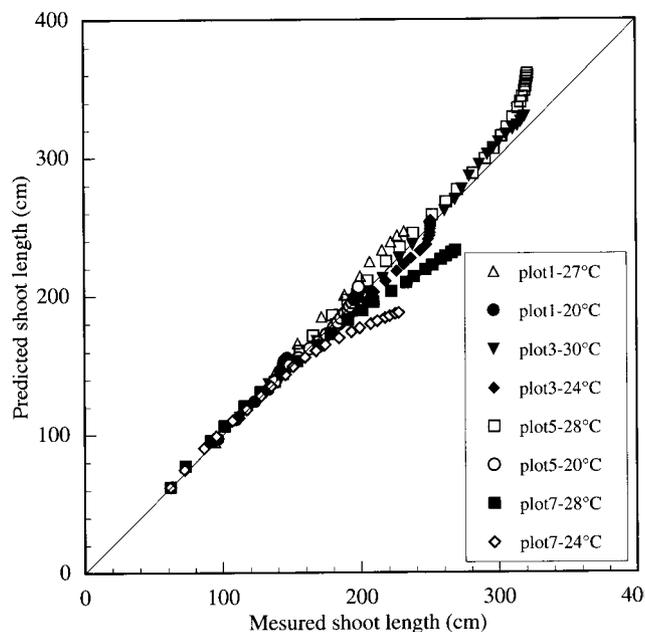


Fig. 4. The relationship between the shoot lengths measured and predicted by the model.

seems to fit the relationship between shoot elongation rate and temperature well. The predicted values of shoot length differed somewhat from the measured values for longer shoot lengths at 28°C in 2000 and, 28°C and 24°C in 2001, since the timing of shoot growth cessation differed between the years studied. It is not clear what causes the difference. However, on the whole, it seems that shoot length predicted by the model fits the measured values well. Therefore, the concept of the model structure seems to be practical. In the future, I will apply this model to field studies on mulberry growth.

References

- Downs, R.J. and Borthwick, H.A. 1956. Effects of photoperiod on growth of trees. *Bot. Gaz.* 117 : 310-326.
- Fukui, K. 2000. Modeling of shoot elongation and leaf unfolding in potted mulberry. *Plant Prod. Sci.* 3 : 410-416.
- Hamada, N. 1933. The effect of photoperiod on mulberry growth. *J. Seric. Sci. Jpn.* 4 : 183-192*.
- Hanks, J. and Ritchie, J.T. 1991. Modeling plant and soil systems. Madison : ASA, CSSA, SSSA. 1-545.
- Heide, O.M. 1974. Growth and dormancy in Norway spruce ecotypes (*Picea abies*) I. Interaction of Photoperiods and temperature. *Physiol. Plant.* 30 : 1-12.
- Horie, T. and Nakagawa, H. 1990. Modeling and prediction of developmental process in rice. I. Structure and method of parameter estimation of a model for simulating developmental process toward heading. *Jpn. J. Crop Sci.* 59 : 687-695**.
- Howe, G.T., Hacket, W.H., Furnier, G.R. and Klevorn, R.E. 1995. Photoperiodic responses of a northern and southern ecotype of black cottonwood. *Physiol. Plant.* 93 : 695-708.
- Ito, D. 1991. A sprouting model in mulberry : From dormancy awakening based on reaction kinetics. *Jpn. J. Crop Sci.* 60 : 47-56**.
- Jones, J.W., Boote, K.J., Jagtap, S.S. and Mishoe, J.W. 1991. Soybean development. Modeling plant and soil systems. In J. Hanks and J.T. Ritchie eds., Modeling plant and soil systems. Madison : ASA, CSSA, SSSA. 71-90.
- Junttila, O. 1976. Apical growth cessation and shoot tip abscission in *Salix*. *Physiol. Plant.* 38 : 278-286.
- Junttila, O. 1980. Effect of photoperiod and temperature on apical growth cessation in two ecotypes of *Salix* and *Betula*. *Physiol. Plant.* 48 : 347-352.
- Junttila, O. 1982. The cessation of apical growth in latitudinal ecotypes and ecotype crosses of *Salix pentandra* L. *J. Exp. Bot.* 33 : 1021-1029.
- Kiniry, J.R. 1991. Maize phasic development. Modeling plant and soil systems. In J. Hanks and J.T. Ritchie eds., Modeling plant and soil systems. Madison : ASA, CSSA, SSSA. 55-69.
- Ritchie, J.T. 1991. Wheat Phasic Development. Modeling plant and soil systems. In J. Hanks and J.T. Ritchie eds., Modeling plant and soil systems. Madison : ASA, CSSA, SSSA. 31-53.
- Summerfield, R.J., Roberts, E.H., Ellis, R.H. and Lawn, R.J. 1991. Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. *Exp. Agric.* 27 : 11-31.
- Taguchi, R. and Kikuchi, S. 1951. A effect of photoperiod on mulberry shoot growth and dormancy. *J. Seric. Sci. Jpn.* 20 : 277*.
- Tollenaar, M., Daynard, T.B. and Hunter, R.B. 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. *Crop Sci.* 19 : 363-366.
- Yan, W. and Wallance, D. 1996. A model of photoperiod x temperature interaction effects on plant development. *Crit. Rev. Plant Sci.* 15 : 63-96.
- Yan, W. and Wallance, D. 1998. Simulation and prediction of plant phenology for five crops based on photoperiod x temperature interaction. *Ann. Bot.* 81 : 705-716.

* In Japanese

** In Japanese with English abstract