Modeling of Mulberry Shoot Elongation and Leaf Appearance in Field Conditions

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Abstract: To predict mulberry (Morus alba L. Shin-ichinose) vegetative growth, I constructed shoot elongation and leaf appearance models for mulberry grown in field conditions. The shoot elongation rate and leaf appearance rate were decided by the product of growth activity (GA) and potential rates (PR) realized at the maximum GA under a given environmental condition. GA is dimensionless and ranges from 0 to 1. GA and PR of shoot elongation rate were determined by temperature, photoperiod and shoot length, and temperature and shoot length, respectively. GA and PR of leaf appearance rate were determined by photoperiod, and temperature, respectively. Model parameters were estimated by an iterative method using five-year mulberry growth data. The values calculated by both models were similar to the measured values and represented annual fluctuation well. These models also showed good estimation of data, which were not used for determining parameters. Therefore, it seems that these models well represent mulberry vegetative growth response to temperature and photoperiod, and are practical.

Key words: Leaf appearance, Model, Morus alba, Mulberry, Photoperiod, Shoot length, Temperature, Tree.

Silkworm feed on mulberry (Morus alba L.). Since the number of silkworm rearing has been encouraged to increase in Japanese sericulture system, time and amount of mulberry harvest have become various. This situation has made old ways of mulberry cultivation became unhelpful for new one. Therefore, it is desirable to establish a new way of mulberry cultivation system suitable for present Japanese silkworm rearing in order to make rearing plans efficiently and profitably. In other crops, prediction techniques of crop developmental state have been used to get products efficiently. Simulation models for predicting the crop developmental state have been developed for many crops, such as rice (Horie and Nakagawa, 1990), wheat (Ritchie, 1991), and maize (Kiniry, 1991). Such simulation models also could be useful for new mulberry cultivation systems and I constructed a simulation model for mulberry vegetative growth in field conditions.

The longest shoot length in a plant has been used as a growth index in mulberry cultivation (Hasegawa, 1969; Yamanouchi et al., 2001), and therefore, in a practical aspect it is important to construct a model of the longest shoot growth. However, leaf appearance is adopted as a developmental index for many crop growth models, since the rate of leaf appearance is closely related to environmental factors such as temperature, photoperiod and others. In mulberry, the leaf number was found to be a better index of mulberry growth than the shoot length due to a closer relationship with temperature (Fukui 2001). Therefore, I also tried to construct a mulberry leaf appearance model to address the biological aspect of mulberry.

The relationship between shoot elongation rate and temperature, and leaf appearance rate and temperature were described by Richard's equation (Fukui 2000b). The rate of shoot elongation increased until the shoot length reached about 100cm, and became stable thereafter (Fukui 2000b). Decrease of shoot elongation rate caused by short photoperiod was simulated by a non-linear regression model (Fukui 2004). In this article, I applied these relationships to shoot elongation and leaf appearance growth of mulberry in field condition, and simulated the growth by linear regression models. After that, fitness of the models was verified.

Material and methods

I investigated the shoot length and leaf number of the longest shoot of mulberry (cv. Shin-ichinose) plants growing in the field condition from 1997 to 2002. The mulberry field (140.1°E, 36.1°N) is 20 m long and 12 m wide, and its soil is volcanic ash. Mulberry plants were planted at 2.0 m inter-row and 0.6 m inter-plant spacing. Half of each of the 10 rows was used as a spring pruning field and summer pruning field. Mulberries in the spring pruning field were cut at stump base only before spring sprouting. Mulberries in the summer pruning field were cut at stump at the start of June and were cut 1.2m above ground at the start of October. Plants received N, P₂O₅,
and K₂O fertilizer at a rate of 15, 6.0 and 7.2 kg 10⁻¹a⁻¹ in March and June every year. About 1 t 10⁻¹a⁻¹ of manure was also supplied to the field every year. In 1997, I used the plants which were planted in 1989 at a density of 17 plants per row. In other years, I used the mulberries that were planted in 1996 at a density of 19 plants per row. Ten plants were examined about every 10 days from 10 May to 30 September in the spring pruning field and from 30 June to 30 September in the summer pruning field. Spring sprouting day was investigated with ten plants in the summer pruning field, and an average of the days was used for determining the mulberry spring sprouting day. Daily temperature was measured at the meteorological field located about 200 m west from the experimental field.

**Results**

Fig. 1 shows the changes in mulberry shoot length and leaf number in the field experiment. Both shoot length and leaf number changed similarly. After sprouting, the rates of shoot elongation and leaf appearance increased gradually and finally became almost 0. To construct shoot elongation and leaf appearance models, I represented the shoot elongation rate and leaf appearance rate as functions of temperature, photoperiod and degree of vegetative growth shown by the shoot length, and determined the functions from past and present results.

The mulberry shoot length and leaf appearance models constructed here follow the design of Fukui (2000b). Shoot length S, and leaf number N, are determined as follows:

\[
S(x) = S(x-1) + s \quad (1)
\]

\[
N(x) = N(x-1) + n \quad (2)
\]

Where S(x) and N(x) are the length of the longest shoot (cm) and the number of leaves that appeared on it, respectively, at the xth day from the initial sprouting day in the spring pruning field and from the first day of measurement in the summer pruning field; and, s and n are the daily shoot elongation (cm day⁻¹) and the number of leaves appearing daily (day⁻¹), respectively. Following the previous report (Fukui 2004), s is written as,

\[
s = PR_s \cdot GA \quad (3)
\]

and the same concept is applied to n,

\[
n = PR_n \cdot GA \quad (4)
\]

where PR(potential rate) s and PR n are defined as the potential rate of shoot elongation and leaf appearance, respectively, realized at the maximum GA (growth activity) under given environmental conditions. GA, and GA s represent the growth activity of mulberry shoot tips. GA and GA s are dimensionless and range from 0 to 1, and the values change from those of the previous day.

As shown in the previous report (Fukui 2004), PR s is a function of temperature. The shoot elongation rate and the leaf appearance rate increase linearly with increasing temperature (Fukui 2000b). Therefore, I applied the linear functions for the relationships between temperature and PR s, and between the temperature and PR n below threshold temperature and described these relationships as constant above the threshold temperature.

GA is also a function of temperature (Fukui 2004). However, I did not determine what kind of temperature relates to GA in the previous report, and this point must be clarified. Fukui (2004) supposed that the average temperature for a certain number of days determines whether the activity of the mulberry shoot tips is promoted or not under short photoperiod conditions. However, in the field experiments of this study, it seems that low temperature of individual day effectively depresses s via GA, (Table 1). After the end of August, the average temperature below 23°C depressed the rate of shoot elongation markedly. The rates in the period Sept.1-Sept.10, in 1998 and 2001
were depressed more markedly than in other years, and the rate in the period Sept.11-Sept.20, 1997, decreased more than in 1999 and 2000. In the same period, the degree of depression of s in 1999 was larger than in 2000 even though the average temperature was higher in 1999 than in 2000. However, the period in 1999 had two days at an average temperature below 22°C and the average temperature of all days in the period was higher than 22°C in 2000 (data not shown). The larger depression of s in 1999 seems to be due to the low temperature of individual day. Therefore, I used daily average temperatures for the temperature related to GA, and applied similar relation to GAn.

The average temperature in the period Sept.11-Sept.20 in 1998 and 2001 was higher than 23°C but s was not increased. From these growth responses to temperature, it seems that mulberry needs long periods at a high temperature to recover the depressed shoot tip activity again. Substantially, the activation effects of a high temperature on s via GA need not be considered in field conditions.

Fukui (2004) showed that the decline of mulberry shoot elongation growth in the fall was due to a short photoperiod and described that GAs is a function of photoperiod and PR s is not. In the current models, the same relationship was applied to the daily shoot elongation s and the number of leaves appearing daily n.

The shoot elongation rate increased until the shoot length reached about 100cm and became stable thereafter, and the leaf appearance rate was treated as independent of degree of vegetative growth from the result of a phytotron experiment (Fukui 2000b). However, the plant height in the phytotron is limited and both rates for above 200cm shoot length are not clear. Table 1 shows a change in the mulberry shoot elongation rate in the spring and summer pruning fields over five years. The rate in the summer pruning field was almost always higher than in the spring pruning field, except for the early mulberry growth period in the summer pruning field. From the results, it seems that the shoot elongation rate decreases gradually from the maximal rate which mulberry can show under given environmental conditions after the shoot length reaches a certain value. Fukui (2004) showed that a decline in s in the fall was due to inactivity of the shoot tips. In the spring pruning field, s, decreased more steeply and the mulberry ceased to grow earlier than in the summer pruning field (Table 1). This growth behavior shows that older mulberry loses shoot elongation activity earlier than younger mulberry. Therefore, I suppose that GA decreases gradually with the advance of growth after the shoot length reaches a certain values. In field conditions, the leaf appearance rate was not different at the same period in spite of different degree of vegetative growth (Table 1). Therefore, I regard the change in the leaf

| Year | Shoot Elongation Rate | Leaf Appearance Rate |
|------|-----------------------|----------------------|
| 1997 | 0.30                  | 0.35                 |
| 1998 | 0.40                  | 0.45                 |
| 1999 | 0.50                  | 0.55                 |
| 2000 | 0.60                  | 0.65                 |
| 2001 | 0.70                  | 0.75                 |

Table 1. Yearly changes in average temperature, and the shoot elongation rate and leaf appearance rate of mulberry plants in spring and summer pruning fields for five years.
appearance rate is constant irrespective of the degree of vegetative growth if environmental conditions are constant.

Since, in the field experiments, mulberry could take up enough chemical nutrients, nutrient factors were not considered in the models. Although I did not irrigate the field, mulberry had no visible drought stress in the experiment period. Therefore, I did not consider the water status in the models.

According to the previous report (Fukui 2004) and above consideration, \( PR_s, GA_s, PR_n \) and \( GA_n \) are written as,

\[
PR_s = PR_{s\text{max}} \cdot f_1(T) \cdot h_1(S) \tag{5}
\]

\[
GA_s(x) = GA_{s(x-1)} \cdot f_2(T) \cdot g_1(L) \cdot h_2(S) \tag{6}
\]

\[
PR_n = PR_{n\text{max}} \cdot f_3(T) \tag{7}
\]

\[
GA_n(x) = GA_{n(x-1)} \cdot f_4(T) \cdot g_2(L) \tag{8}
\]

where \( PR_{s\text{max}} \) and \( PR_{n\text{max}} \) are the maximum rate of shoot elongation and the maximum rate of leaf appearance, respectively; \( T \) (°C) is the daily average temperature; \( L \) (hour) is the daily photoperiod; Functions are represented by \( f_1-4(T) \), \( g_1-2(L) \) and \( h_1-2(S) \). \( f_1-4(T) \) and \( g_1-2(L) \) are defined as linear functions. A quadratic function instead of a sigmoid function is used for \( h_1(S) \) to simplify model equations. Although the shape of

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**Fig. 2.** Correlation of measured shoot length and leaf number with the values calculated by the model. A, shoot length in the spring pruning field; B, shoot length in the summer pruning field; C, leaf number in the spring pruning field and D, leaf number in the summer pruning field. The symbols, □, ○, △, ◇, ▽ and ■ show data for 97, 98, 99, 00, 01 and 02, respectively.
Each function was written as,

\[ f_1(T) = a_1 \cdot (T - b_1) + 1 \]  
\[ f_2(T) = a_2 \cdot (T - b_2) + 1 \]  
\[ g_1(L) = a_3 \cdot (L - b_3) + 1 \]  
\[ h_1(S) = -0.25 \cdot a_4 \cdot S^2 + a_4 \cdot S \]  
\[ h_2(S) = a_5 \cdot (S - b_5) + 1 \]  
\[ f_3(T) = a_6 \cdot (T - b_6) + 1 \]  
\[ f_4(T) = a_7 \cdot (T - b_7) + 1 \]  
\[ g_2(L) = a_8 \cdot (L - b_8) + 1 \]

where \( a_{1-8} \) and \( b_{1-8} \) are parameters. For all linear functions, if the functions drop below 0, they are defined as 0, and if the functions exceed 1, the functions are defined as 1. \( h_1(S) \) is defined as 1 if \( S \) is beyond \( 2 \cdot a_4 \). To avoid the short-photoperiod effect on \( G_A \) and \( G_{A_n} \) for the early stage of vegetative growth in the spring pruning field, \( G_A \) and \( G_{A_n} \) are defined as 1 below 50cm shoot length, and 30 in leaf number, respectively. Since \( f_3(T) \) and \( f_4(T) \) represent an interaction effect with photoperiod on \( G_A \) and \( G_{A_n} \) (Fukui 2004), \( f_2(T) \) and \( f_4(T) \) become effective in the model after photoperiod \( L \) becomes below \( b_3 \) or \( b_8 \), respectively.

All parameters were estimated by an iterative method, using data from 1997 to 2001. I used 1 and 0 for the first shoot length and leaf number values, respectively, in the spring pruning field data, and the first measured shoot length and leaf number values in the summer pruning field data. The first values of \( G_A \) and \( G_{A_n} \) were set at 1. Estimated parameters are shown in Table 2. \( b_1 \) is about 1.5°C lower than that in the phytotron experiment 27°C (Fukui, 2000b). \( b_6 \) is also lower than the experimental result (Fukui, 2000b). However, the value of \( b_6 \) is not bad because there are only 6 days at which the average temperature was beyond the \( b_6 \) value in 5 years. The photoperiods of \( b_3 \) and \( b_8 \) correspond to the photoperiods at Aug. 15 and Sep. 3, respectively. These days seem to be in accordance with true values. Since \( a_7 \) was almost 0 and \( f_4(T) \) was almost 1, \( G_{A_n} \) depended on only the photoperiod. A coefficient of the variation of values calculated by the shoot elongation model was a little larger than that calculated by the leaf appearance model. Both the shoot length and the number of leaves appearing calculated by the model fitted the measured values well and showed annual differentiation of measured values well (Fig. 2 and 3). Fig. 4 shows changes in \( G_A \). Sudden depression of \( G_A \) after September corresponds to a low temperature below \( b_2 \) and the effects of the degree of vegetative growth and photoperiod gradually depressed \( G_A \). The changes in \( G_A \) represented the depression of shoot elongation rate well. Fig. 2 also shows the predicted

![Fig. 3. Comparison of measured and calculated values of final shoot length (A) and leaf number (B). The symbols, ■ and □ shows measured and calculated values, respectively, in the spring pruning field. The symbols, ▲ and △ shows measured and calculated values, respectively, in the summer pruning field.](image-url)
values of shoot length and number of leaves appearing in 2002, whose data was not used for deciding the parameters of the models. Since the models provided a good estimation for 2002 data, the constructed models are practical and the concept of the current model structure seems to be appropriate.

Discussion

Since the responses of the shoot elongation rate to inner and outer factors are different from the leaf appearance rate, there are structural differences between the shoot elongation model and the leaf appearance model. The shoot elongation rate depends on the degree of vegetative growth but leaf appearance rate does not. The depression of the shoot elongation rate in the spring pruning field was much earlier than in the summer pruning field, while the difference in the leaf appearance rate was small. These differences made the former model more complex than the later. The leaf appearance rate is constant at constant environmental conditions in many plants (Warrington and Kanemasu, 1983; White et al., 1990; Kirk and Marshall, 1992) and the rate increases linearly with increasing temperature (Hofstra et al., 1976; Leong and Ong, 1983; Kirk and Marshall, 1992). Warrington and Kanemasu (1983) showed that constancy of the leaf appearance rate in corn reflects a constancy of the leaf initiation rate in constant conditions. If this concept is applied to mulberry, the simple structure of the leaf appearance model is due to a simple response of leaf initiation to environmental factors. On the other hand, the shoot elongation rate relates not only to cell division but also to cell growth. Cell growth seems to be the cause of the more complex structure of the shoot elongation model. If the leaf appearance rate is related to only cell division, the parts of the shoot elongation model, \( f_2(T) \), \( h_1(S) \) and \( h_2(S) \), which are not included in the structure of the leaf appearance model, are related to cell growth and seem to be the cause of less precision of shoot elongation prediction than number of leaves appearing.

There are a few reports about the prediction of the longest shoot length of mulberry (Suzuki and Kanaya, 1981; Kato and Inoue, 1998). In such reports, the length on a specific day was regressed with meteorological factors and predicted by the regression equations. Therefore, it is impossible for these equations to predict it at an arbitrary day. The model for the length in the present article is able to predict it on an arbitrary day and the predicted values in 2002 are similar to measured values at any time (Fig. 2). Therefore, the constructed model is more practical and useful.

The biggest cause of variance of values calculated by the shoot elongation model seems to be the wind. The measured shoot length in the late period of the summer pruning field in 2001 was about 20cm shorter than the calculated length. Since we had a storm with strong winds in this year, many mulberry shoots were flexed by the wind. Especially, mulberry plants in the summer pruning field were damaged seriously. The last measured leaf number was only four lower than the calculated number in the same mulberry field. This fact shows that shoot flex has a higher effect on the shoot elongation rate than the leaf appearance rate. The effects of storm winds are unpredictable and it is extremely difficult to quantify the degree of these effects on shoot growth. For precise prediction of the shoot elongation model, it is important to handle such data adequately.

In the future, I will try to apply the models to a broader area and in various cultivation systems. For precise application, other factors need to be considered. Nutrition storage and water conditions also seem to be important. Ohyama (1970) showed that strong harvest stresses reduce shoot growth. The shoot elongation rate of mulberry saplings (Fukui, 2000a) was lower than the rate of three years old mulberry (Fukui, 2000b). These facts show that shoot elongation rate depends on the amount of stored nutrition. Since, in this article, the growth rate of the summer pruning field, which had stronger harvest stress, is similar to that of the spring pruning field, it seems that the amount of stored nutrition had little effect on mulberry growth in the current field experiments. However, the amount of stored nutrition may have an important role in mulberry growth when the model is applied to mulberry, which accepts stronger harvest stress, for example, three prunings a year. To introduce nutrition storage factors into the model, however, we need to construct a way to evaluate nutrition storage conditions in mulberry and to quantify the relationship between the shoot elongation...
rate and nutrition storage conditions.

Ohyama (1966) investigated the relationship between the growth of mulberry planted in pot and soil moisture, and showed that shoot elongation growth was depressed by low soil moisture. Since mulberry is a tree, tolerance to drought stress seems to increase with the development of the root system from year to year, according to mulberry growth data in field conditions (Naoi, 1977). The mulberry did not show visible drought stress response in the current experiments. However, it is possible that the mulberry growth was depressed invisibly by light drought stress and that some variance of values calculated by the models was due to such drought stress. Although Matthews and Stephens (1998) used saturation deficit as a variable for their tea shoot elongation model, there has been no data about the effect of saturation deficit on mulberry growth. To apply the models to various areas, it is important to investigate the effects of water on mulberry growth. However, it is necessary to quantify the effect of water on mulberry growth.

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