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A Simulation Approach for the Determination of the Optimum Leaf Area Index in a Mulberry Population

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Abstract

The value of the optimum leaf area index (*LAIopt*), at which the net photosynthesis of a population (*Pp*) or foliage (*Pf*) was maximized, was investigated for mulberry using the simulation program designated as MORUS-LICS, in which a model mulberry population is generated and its light-intercepting conditions and net photosynthesis are predicted through the method of numerical experiment. Under the averaged radiation and temperature conditions in Central Japan in July and September, simulations predicted that the *LAIopt* was never constant and depended on the planting density. In a normally planted population, *Pp* increased until the time when the longest shoot length (*LSL*) and *LAI* reached values of 210 cm and 8.5, respectively, and thus the *LAIopt* could not determined in the course of shoot elongation. However, it was predicted that *Pf* would increase slightly by pruning when the *LSL* exceeded 150 cm. In this case, the *LAIopt* after pruning was in the range of 4.9-5.8. The densely planted population, on the contrary, became over-luxuriant at 120 cm *LSL (LAI* = 6.1), and *Pp* stopped increasing. Moreover, *Pf* showed a considerable increment when the population with an *LSL* of 120 or 150 cm was pruned. The *LAIopt* values after pruning were 3.8 or 5.1, respectively.

Discipline: Sericulture/ Agro-meteorology
Additional key words: light-intercepting condition, photosynthesis

Introduction

Monsi and Saeki[5,6] developed a theoretical method for the calculation of the photosynthetic rate of a population (P) using the leaf area index (LAI), light intensity (I), light extinction coefficient (K), leaf respiration rate (r) and 2 parameters of the light-photosynthesis curve of a leaf (a, b), and then predicted the existence of the optimum leaf area index (LAI_{opt}) which maximizes P under given I, K, r, a and b. Therefore, it has been a major cause for concern to confirm whether the LAI_{opt} exists or not, and what value it would have if it existed, especially for a leaf crop like mulberry. Using this method, Masuda and Kono[4] estimated the LAI_{opt} for a mulberry population at 7.0. However, leaves must be distributed at random in the horizontal direction to adopt this method, while the inter-row distances of Japanese mulberry fields are generally around 2 m, and the leaf distribution is far from random at the early growth stage.

To replace Monsi and Saeki's method, the author developed a simulation program designated as MORUS-LICS which estimates P for a mulberry population[2]. This paper describes this program and presents the results obtained for LAI_{opt}.

Simulation program

1) *Outline*

The program MORUS-LICS is composed of 2,000 lines described in FORTRAN 77 language. It predicts the light-intercepting conditions and net photosynthesis of a model mulberry population through the method of numerical experiment. As shown in the flow chart (Fig. 1), it first defines the geometrical model of a mulberry population according to the inputted initial conditions, and then generates a beam and solves simultaneous equations to determine where the beam is captured. After the generation of many beams, it calculates the amount of photosynthesis

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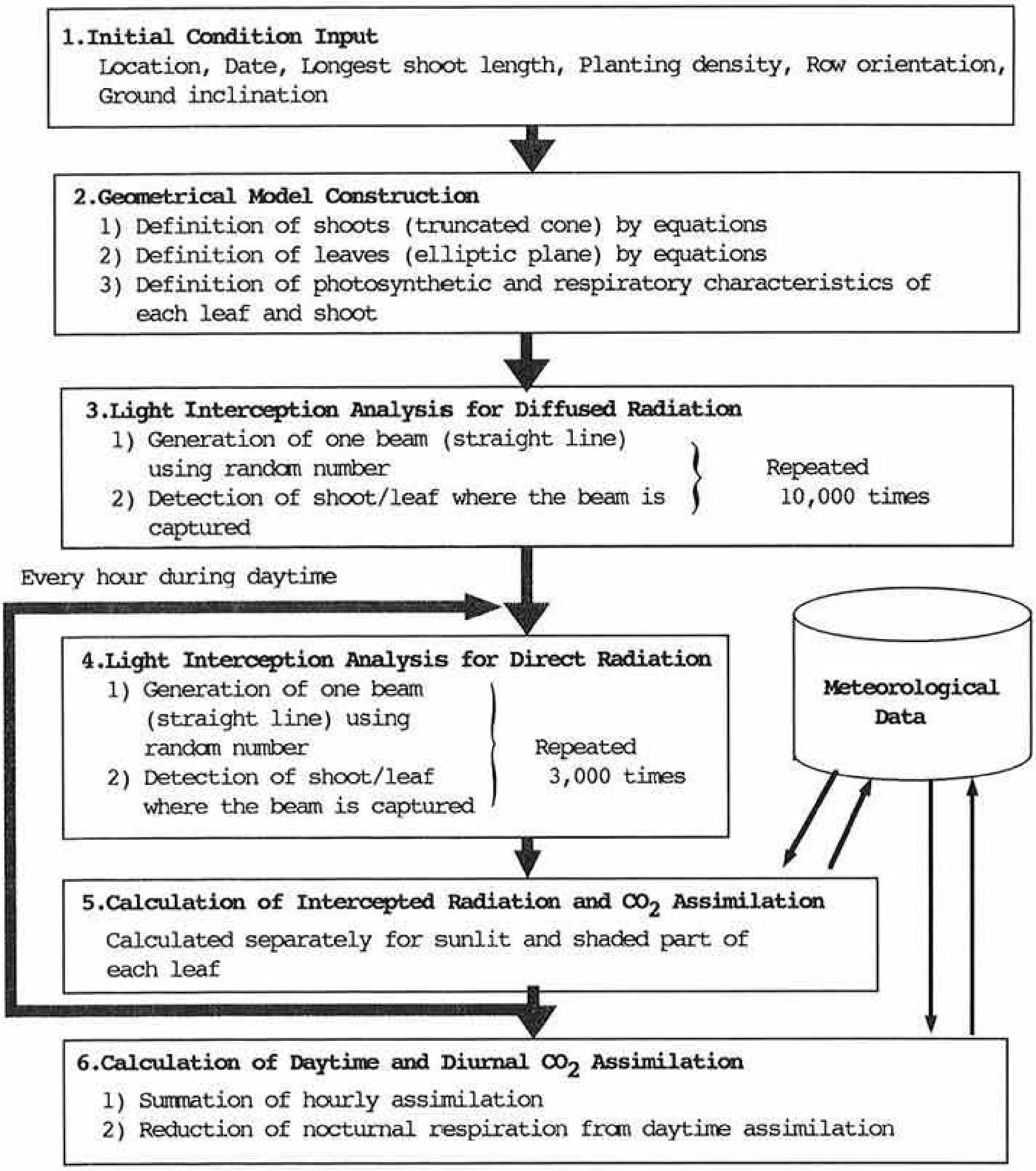

Fig. 1. General flow chart for MORUS-LICS

and respiration for each stem/leaf. We can select the planting density, row orientation, longest shoot length (*LSL*), etc. as initial conditions. It is also possible to 'prune' the model population.

2) *Geometrical model of mulberry population*

In MORUS-LICS, 2 populations with a different planting density can be selected as an initial condition: normally planted population (NPP) with inter-row and inter-plant distances of 2.0 and 0.6 m, and densely planted population (DPP) with 1.0 and 0.5 m distances. The model tree in the population is composed of a stump, 30 (NPP) or 15 (DPP) stems and many leaves.

In the model tree, stems are defined as circular truncated cones and are classified into 4 types differing in elongation. They develop from the upper edge of the stump which is defined as a circular truncated cylinder. Leaves are modeled as elliptic planes attached to the stem with a straight linear petiole (Fig. 2-A). Length, width, azimuth angle, inclination angle, etc. of each stem/leaf must be determined to describe their figures as equations in the proper position. These values depend on *LSL* and are given based on the measured data.

The procedure to determine the stem/leaf distribution of the whole population from a single model tree is illustrated in Fig. 2. In MORUS-LICS, all

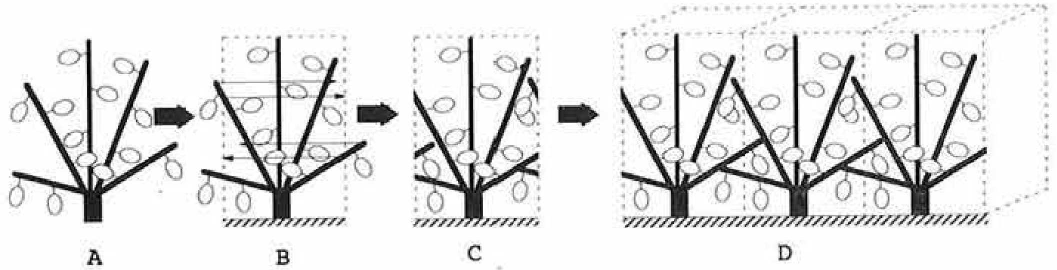

Fig. 2. Procedures to determine the spatial stem and leaf distribution of a population from a single model tree

the trees of the model population are assumed to display the same form. Thus the whole population is represented as a simple continuation of a rectangular prism, when the ground is horizontal (Fig. 2-D). To determine the stem/leaf distribution in this rectangular prism (unit population), MORUS-LICS first describes the model tree in the center of the unit population (Fig. 2-B) and then applies parallel translation treatments to the stems/leaves if they occur outside of the unit population (Fig. 2-C). The vertical distribution of stems/leaves of the model population agreed well with the distribution determined in the field[2].

3) Light interception analysis

To analyze the light-intercepting conditions, a straight line representing a beam was first determined. This line passes a point selected at random on the upper wall of the unit population. Its direction cosine is determined using a random number so as to originate uniformly from the hemisphere in case of diffused radiation, while it is determined by the position of the sun in case of direct radiation. Then, the equation of the beam is solved simultaneously with the equation of a stem/leaf, to determine whether the beam is intersected by the stem/leaf. If the beam is intersected by more than one stem/leaf, it is considered to be captured by the stem/leaf whose intersection point is the highest above the ground. These procedures are repeated 10,000 times for diffused radiation, whereas 3,000 times every hour for direct radiation because the position of the sun changes with time. Finally, we can determine how many times beams are intercepted by each stem/leaf or in each stratum.

4) Calculation of photosynthesis and respiration

In MORUS-LICS, photosynthetic and respiration rates of leaves are affected not only by the leaf irradiance but also by the air temperature, leaf age and the date of unfolding. Therefore, calculations of the amount of photosynthesis and respiration are performed for each leaf, dividing it into sunlit and shaded part. Meteorological data required for the calculation are derived from the database, according to the date and location inputted as initial conditions. Respiration of stems is also calculated similarly.

Initial conditions

First, to analyze how light interception and population photosynthesis change with shoot elongation, simulations were made under various *LSL* both for NPP and DPP. Next, to analyze the effect of pruning, the populations with *LSL* of 120, 150, 180 and 210 cm were subjected to 'pruning' at various heights. Row orientation and ground inclination were fixed in the north-south and horizontal directions, respectively. The averaged values of radiation and temperature in July and September in Central Japan were used in the calculation of photosynthesis and respiration. The photosynthetic and respiration parameters of the stem/leaf were assumed to remain unchanged by pruning.

Results and discussion

1) LAI_{opt} in the course of shoot elongation

Simulated net photosynthesis of the population throughout the day (P_p) is shown in relation to *LSL* (Fig. 3) and *LAI* (Fig. 4). In NPP, P_p continued to increase linearly with *LSL* and *LAI* until they reached values of 210 cm and 8.5, respectively. However, in DPP, P_p once stopped increasing at 120 cm *LSL* and then increased again slowly.

Vertical patterns of light penetration, leaf irradiance and CO_2 budget in DPP were compared with those in NPP (Fig. 5). When the *LSL* was 60 cm, DPP showed a higher leaf irradiance, caught more light and thus acquired 13% more P_p compared with NPP. However in a DPP with 120 and 180 cm *LSL*,

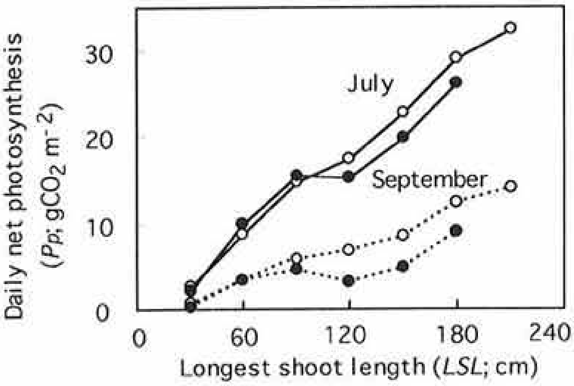

Fig. 3. Diurnal net photosynthesis of the population (P_p) in relation to the longest shoot length (*LSL*)
○ : NPP, ● : DPP.

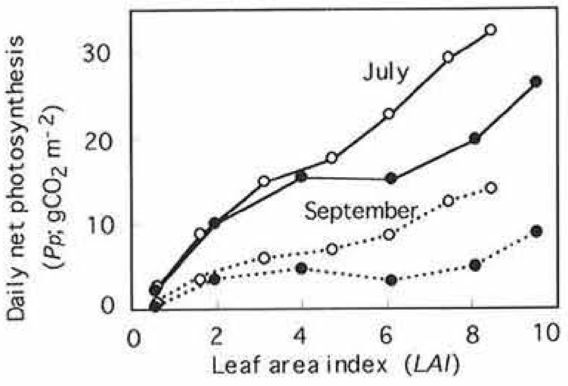

Fig. 4. Diurnal net photosynthesis of the population (P_p) in relation to *LAI*
○ : NPP, ● : DPP.

almost all the light was intercepted in the top layer and the CO_2 budget in the lower layers became negative. In the case of NPP, light was still delivered to the lowest layer even at 180 cm *LSL* because of the wide inter-row space, and the CO_2 budget remained positive in almost all the stratum. At 120 and 180 cm *LSL*, P_p was lower in DPP by 10-13% compared with NPP.

Based on the theory of randomly distributed foliage[5,6], photosynthesis should be exactly balanced with respiration in the lowest stratum if the *LAI* of the foliage is optimum. Therefore, we can conclude that DPP in this study reached an over-luxuriant status at 120 cm *LSL* (*LAI* = 6.1), because the CO_2 budget in the lower layers became negative and P_p stopped increasing. However, the NPP was not in

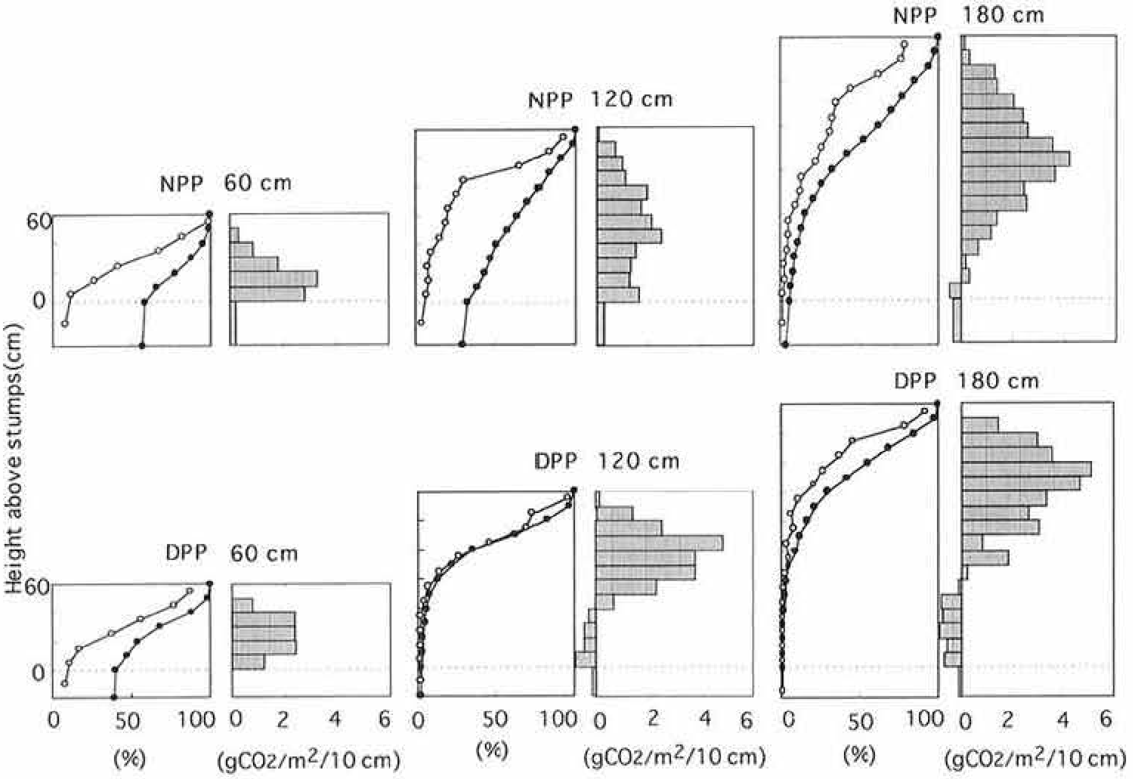

Fig. 5. Vertical pattern of light penetration, leaf irradiance and CO_2 budget in NPP and DPP at 60, 120 and 180 cm *LSL* in July
● : light penetration, ○ : leaf irradiance, ▨ : CO_2 budget.

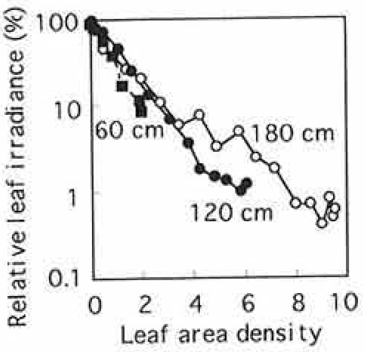

Fig. 6. Relationship between relative leaf irradiance and leaf area depth in DPP with 60, 120 and 180 cm *LSL*

an over-luxuriant status even at 210 cm *LSL* (LAI = 8.5), because the CO_2 budget in the lower layers almost remained positive and P_p continued to increase.

Monsi and Saeki[5,6] also predicted that P would decrease with *LAI* after the population reached the over-luxuriant status. However in this study, P_p in DPP once stopped increasing at 120 cm *LSL* but then increased slowly again with the increase of *LSL* and *LAI*. To analyze this phenomenon, the relationships between leaf irradiance and leaf area depth at 60, 120 and 180 cm *LSL* are presented in Fig. 6. The leaf irradiance in the middle and lower layers was larger for 180 cm *LSL* than for 120 and 60 cm *LSL* for the same leaf area depth, indicating that the light-intercepting condition in the lower layers was gradually improved with shoot elongation. The same phenomenon was reported in a densely planted mulberry field[4] and in a natural plant population. This may account for the fact that P_p in DPP continued to increase even under over-luxuriant conditions.

2) LAI_{opt} *in case of pruning*

Simulated net photosynthesis of the foliage during the daytime (P_f) in NPP and DPP with 120, 150, 180 and 210 cm *LSL* pruned at various heights is shown in relation to the height of pruning (Fig. 7) and *LAI* after pruning (Fig. 8). In DPP, it was predicted that P_f would increase markedly to 1.3 - 1.7 times by pruning at optimum height (H_{opt}), which occurred at about half the original *LSL*. LAI_{opt} was also identified and varied from 3.8 to 6.1 depending on the original *LSL*. On the other hand, H_{opt} was not as clearly defined in NPP, and could be determined at about half the original *LSL* only when the *LSL* exceeded 150 cm. P_f increased only by 1.1 - 1.2 times at maximum. LAI_{opt} varied from 4.9 to 5.8 depending on the original *LSL*.

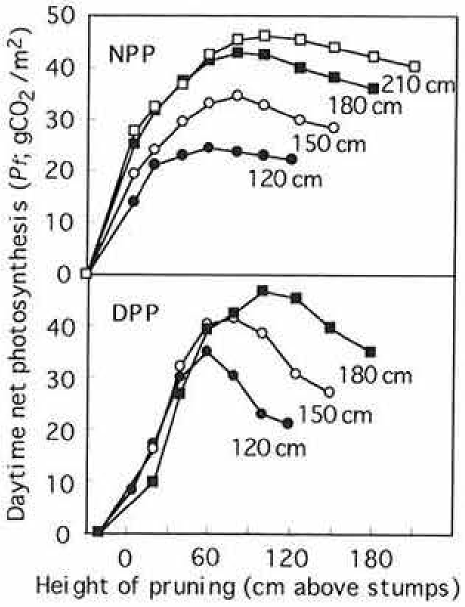

Fig. 7. Daytime net photosynthesis of the foliage (P_f) in NPP and DPP pruned at various heights
Numerals indicate the *LSL* before pruning.

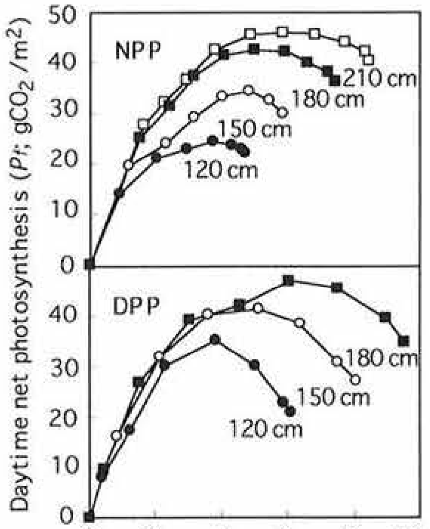

Fig. 8. Daytime net photosynthesis of the foliage (P_f) in NPP and DPP in relation to the *LAI* after pruning
Numerals indicate the *LSL* before pruning.

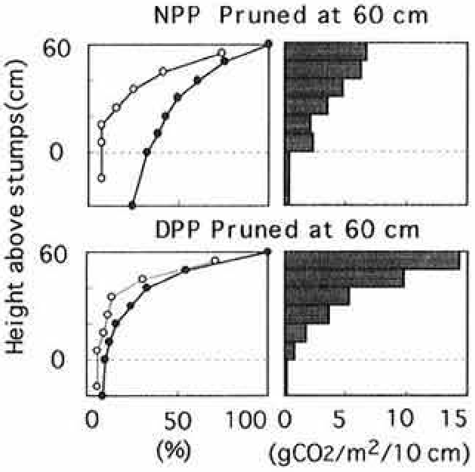

Fig. 9. Vertical pattern of light penetration, leaf irradiance and CO_2 budget in NPP and DPP with 150 cm *LSL* pruned at 60 cm
See the notes in Fig. 5.

To analyze the effect of pruning more precisely, vertical patterns in light penetration, leaf irradiance and CO_2 budget in DPP with 150 cm *LSL* pruned at 60 cm were compared with those in NPP (Fig. 9). In DPP, the over-luxuriant growth conditions were alleviated by pruning, because active assimilation began in the strata where the CO_2 budget had been negative. P_f increased by 48% by pruning, and was higher than that of NPP by 18%. In NPP, on the contrary, the light-intercepting condition deteriorated by pruning. Although as much as 25% radiation reached the ground without being intercepted by the population, leaf irradiance in the lower layers was almost the same as that in DPP. It is interesting to note that P_f increased by 17% by pruning (Fig. 7) in spite of the limitation mentioned above, presumably due to the elimination of the juvenile leaves in the upper layers, which show a low photosynthetic ability but intercept a considerable amount of radiation.

Concluding remarks

The present study showed that the value of LAI_{opt} was never constant and depended considerably on the planting density.

In NPP, LAI_{opt} could not be determined in the course of shoot elongation, because the population with 210 cm *LSL* ($LAI = 8.5$) was still not luxuriant enough. However, it was predicted that P_f would increase slightly by pruning when *LSL* exceeded 150 cm. Therefore, the author suggests that NPP should be harvested after *LSL* reaches a value of 150 cm. In this case, the LAI_{opt} after harvest corresponded to 4.9–5.8.

On the contrary, DPP was in an over-luxuriant status as soon as *LSL* reached a value of 120 cm ($LAI = 6.1$). Moreover, considerable increment of P_f was predicted when the population with 120 or 150 cm *LSL* was pruned to about half of the original *LSL*, because over-luxuriant conditions were alleviated. Therefore, the author suggests that DPP should be harvested when *LSL* reaches values of 120 or 150 cm. In these cases, LAI_{opt} after harvest corresponded to 3.8 and 5.1, respectively.

Generally in Japan, mulberry trees are subjected to shoot harvest once or twice during the rearing season from May to October. However, recently in DPP, a higher yield has been achieved in field experiments by harvesting more frequently at earlier growth stages[1,3,7]. This harvesting scheme for DPP seems suitable from the viewpoint of *LAI* regulation, because over-luxuriant growth condition can be alleviated. However, in these experiments, the height of pruning was set at 30–50 cm above the ground to introduce a harvesting machine. It must be noted that such a pruning at low height may not be suitable for foliage photosynthesis (Fig. 7).

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