# チャ葉の光合成阻害における光と低温の相互作用


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# Interaction of Light and Low Temperature in Depression of Photosynthesis in Tea Leaves*

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The growth of new shoots in the first flush of tea depends on photosynthesis in over-wintered leaves[5]. However, net photosynthesis in tea decreased by 40 to 60% of the maximum rate on exposure to winter cold, with partial recovery in early spring[2,8]. Cold-induced depression of photosynthesis is more severe in light than in darkness, and in some cases injury is only observed in light[4,6,7,9,10]. The colour of overwintering tea leaves changes from dark-green becoming reddish or yellowish during the winter, while leaves which have been shaded by other leaves remain dark-green. Thus, light might accelerate cold-induced depression of photosynthesis in overwintering tea leaves. This study was conducted to determine the interaction of light and low temperature in the depression of photosynthesis.

In tea cultivation, shading materials have often been used to improve the quality of green tea or to protect it from frost injury in the spring. These shading materials could easily be used to protect against cold-induced depression of photosynthesis. If inhibition of photosynthesis could be avoided by artificial shading, the yield of tea would increase, since the growth of new shoots in the first flush depends on photosynthesis in overwintered leaves. The author investigated the effects of shading using lawn cloth on the growth of new shoots in the first flush of tea.

## Materials and Methods

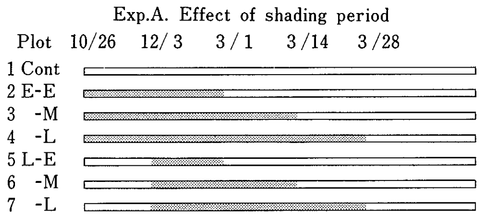
*Conditions experienced by plants used in various experiments*

*Exp. 1 Shading of artificially chilled leaves and field-grown leaves*

Leaf discs or single mature leaves, which were harvested from field-grown tea plants (cv. Yabukita), were floated on distilled water in a chamber at 12℃ for two days. The light intensity was modulated by shading using black lawn cloth and by changing the distance between leaf and light source. Experiments were carried out in spring and in autumn. As for field-grown leaves, mature tea plants (cv. Hatsumomiji) were shaded using black cloth (61.5% shading) from Nov. 13 to Jan. 16.

*Exp. 2 Effects of shading on growth of new shoots in first flush of tea*

Mature tea plants (cv. Yabukita) were used. They were planted every 40 cm in 10 to 15 m-long hedges forming arc-shape bushes. In early October, they were skiffed (lightly




Exp.B. Effect of shading ratio

| Plot | Shading material | Shading rate |
|---|---|---|
| 1 | Unshaded | 0 % |
| 2 | White lawn cloth (F-2000, one layer) | 8 % |
| 3 | White lawn cloth (F-1000, one layer) | 16 % |
| 4 | White lawn cloth (F-1000, two layers) | 32 % |
| 5 | Black lawn cloth (#610, one layer) | 60 % |
| 6 | Black lawn cloth (Black, one layer) | 90 % |

Fig. 1. Protocol for shading treatment in field-grown plants.
Exp. A. Canopy surface directly shaded using black lawn cloth (38.5% shading of full sun irradiance) from Oct. 26 or Dec. 3, 1982 to Mar. 1, Mar. 14 or Mar. 28, 1983, respectively. ▭ unshaded ; ▩ shaded.
Exp. B. Canopy surface directly shaded from Nov. 15, 1983 to Mar. 21, 1984, using different shading ratio (8—90%).

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* Parts of this work were presented at the 177th and 179th meeting of the Crop Science Society of Japan held in April, 1984 and April 1985, respectively.

Table 1. Leaf position and cold-induced depression of photosynthesis.

| Sampling date | Maximum photosynthetic rate ($\mu$moles $O_2/dm^2 \cdot hr$) in | |
|---|---|---|
| | surface leaves | 2nd and 3rd leaves |
| Feb. 3 | 23.0 | 37.4 |
| Feb.27 | 24.1 | 68.6 |
| Mar.13 | 68.9 | 118.3 |

Material : cv. Yabukita.

pruned) to produce an even canopy surface. They were shaded at different times and to various extents as shown in Fig. 1.

*Measurement of photosynthetic rate*

Leaf photosynthesis was determined by measuring the rate of $O_2$ evolution from leaf slices using an oxygen electrode (Rank Brothers, England) at 25℃[1]. $CO_2$ concentration and light intensity were maintained at the saturation levels (40 mM and 80 klx, respectively). The initial slopes of the light-photosynthesis curve and the $CO_2$-photosynthesis curve were measured using the same equipment.

*Measurement of Hill activity and cellular components*

Light saturated Hill actdvity and contents of chlorophyll and fraction-1 protein were measured as described previously[2,3].

*Measurement of winter bud and new shoot growth*

Length and number of leaf initials inside the winter buds were measured for 20–30 winter buds. Transections of the winter buds were prepared and the number of leaf initials were counted microscopically. The yield of new shoots (g dry weight) in the first flush of tea was measured for a 20×20 cm area of canopy. Measurements were repeated 5 to 6 times.

## Results

*Exp. 1 Shading of artificially chilled leaves and field-grown leaves*

The photosynthetic rate of overwintering leaves was suppressed by winter cold and was lowest in February[2]. As shown in Table 1, the second and third leaves, which were shaded by other leaves, were less suppressed than the uppermost leaves positioned on the canopy surface. Taken with the fact that the leaf colour of shaded leaves did not change during winter, this suggests that cold injury is affected by light intensity. The effect of shading on

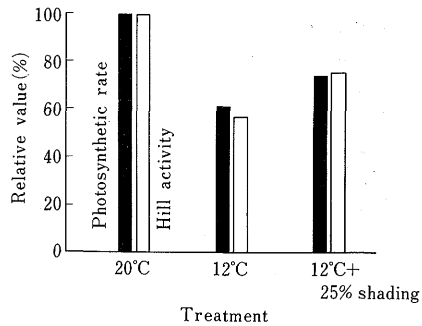


Fig. 2. Effect of shading on cold-induced depression of maximum photosynthetic rate and light-saturated Hill activity. Single leaves were floated on distilled water for two days at 20℃ (cont) or 12℃ (chilling) and shaded using black lawn cloth to 25% of full light intensity, 12 klx. Experiments were carried out in spring and in autumn. ■, rate of photosynthetic $O_2$ evolution; □, light saturated Hill activity. Material: cv. Yabukita.

cold-induced depression of photosysthesis was investigated under controlled environmental conditions.

When single leaves were floated on distilled water and chilled at 12℃ in light (12 klx) for two days, the maximum rate of photosynthesis and the light saturated Hill activity decreased to about 60% of the control value (Fig. 2), although chlorophyll content did not change (96.7–98.5% of control after chilling). These results are consistent with previous results[3]. Twenty five % shading ameliorated chilling injury and the maximum rate of photosynthesis and the light saturated Hill activity remained at 74 and 76% of their control values, respectively. The effect of shading ratio on the suppression of chilling injury is shown in Fig. 3. Even 8% shading reduced photosynthetic depression while the effect saturated at about 50% shading.

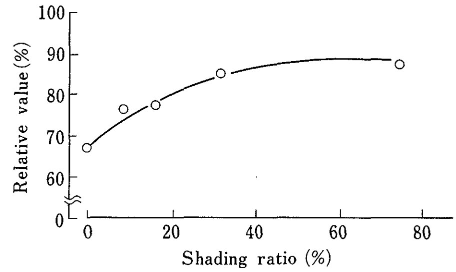


Fig. 3. Effect of shading ratio on cold-induced depression of maximum photosynthetic rate.
Leaf discs were floated on distilled water and chilled at 12℃ for two days. Shading ratio was changed using black lawn cloth and by changing the distance between leaf and light source. Full light intensity was 12klx. Maximum rate of photosynthetic $O_2$ evolution of chilled leaves is shown as percentage of value for unchilled leaves. Material : cv. Yabukita.

The effect of shading on cold-induced depression of photosynthesis was also investigated in field-grown tea plants (Fig. 4). When tea plants were shaded using black lawn cloth (61.5% shading) between Nov. 13 and Jan. 16, the photosynthetic rate of overwintering leaves was higher than in control plants (Fig. 4a). Light staurated Hill activity also showed higher values (Fig. 4c), while fraction–1 protein content remained at a lower level (Fig. 4b). This is consistent with previous results[2,3] implying that photosynthetic depression is mediated through photosynthetic light reactions rather than dark reactions.

Changes in the photosynthetic rate of naturally shaded leaves and the effect of artificial shading in controlled environment and field experiments demonstrate that light accerelates cold-induced depression of photosynthesis in overwintered tea leaves.

*Exp.2 Effect of shadiading on the growth of new shoots in the first flush of tea*

The above observations (Exp.1) suggest that artificial shading modulates cold-induced depression of photosynthesis. Since the growth of new shoots in the first flush of tea depends on photosynthesis in overwintered leaves, it is interesting to examine whether artificial shading inflluences the growth of new shoots. For this purpose, tea plants were shaded according to the protocol shown in Fig. 1.

Fig. 5a shows that when tea plants were shaded using black lawn cloth (61.5% shad-

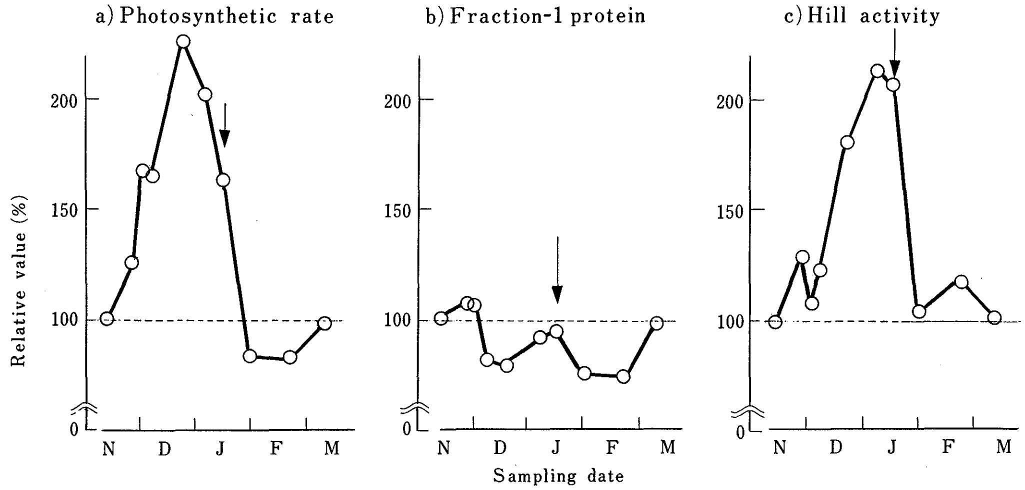


Fig. 4. Effect of shading on maximum photosynthetic rate, fraction–1 protein content and light-saturated Hill activity in field-grown plants.
Canopy surface was directly shaded using black lawn cloth (38.5% shading of full sun irradiance) from Nov. 13 to Jan. 16. Figure shows percentages of values for unshaded leaves.
a, rate of photosynthetic $O_2$ evolution ; b, content of fraction–1 protein ; c, light-saturated Hill activity. Shading removed at the time indicated by arrows. Material : cv. Hatsumomiji.

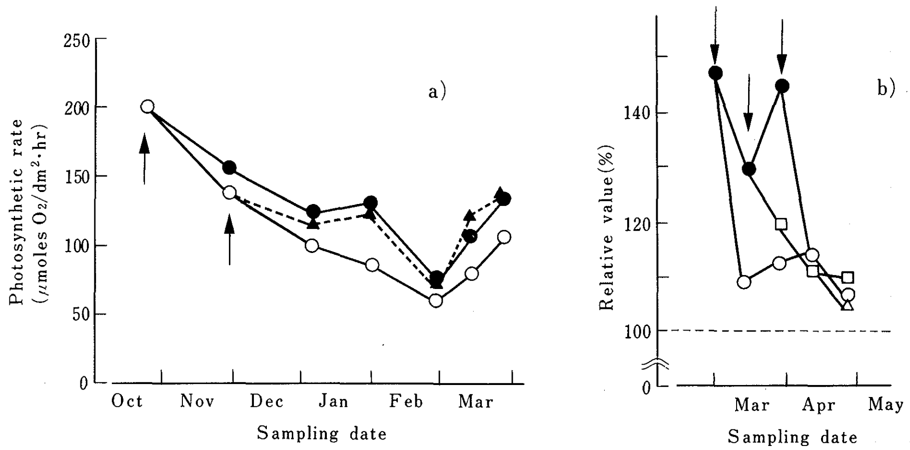


Fig. 5. Effect of shading on protection from the cold-induced depression of maximum photosynthetic rate (Experiments conducted according to Exp. A in Fig. 1).

a : During shading treatment. ○, control (plot no. 1); ●, early shading (plot no. 2, 3, 4); ▲, late shading (plot no. 5, 6, 7). Shading started at time indicated by arrows.

b : After removal of shading in early shading plants. Rate of photosynthetic $O_2$ evolution in early shaded plants expressed as percentage of value for unshaded leaves. Shading removed on Mar. 1 (plot no. 2, ○), Mar. 14 (plot no. 3, □) and Mar. 28 (plot no. 3, △) as indicated by arrows. ● ; Photosynthetic rate of shaded leaves. Material : cv. Yabukita.

ing) on Oct. 26 or Dec. 3, the maximum rate of photosynthesis in overwintering leaves remained at higher values than in control plants. Fig. 5b shows that when shading in early shaded plants was removed on Mar. 1, 14 or 28, the photosynthetic rate sharply decreased but remained at higher value than in control plants (103–120%). Although data are not shown in the figure, when shading in late shaded plants was removed on Mar. 1, 14 or 28, the effect was essentially the same (106–121% of control).

Fig. 6 shows the effect of shading ratio on protection from cold-induced depression of photosynthesis. When the maximum rate of photosynthesis was measured on Dec. 15, the protection from injury to photosynthesis was almost parallel to the shading ratio. Marked protection effect was observed on Feb. 6 and Mar. 21 by 60% shading. However, further increase in the shading ratio reduced the extent of protection. After the removal of shading (16–60%), photosynthetic rates were higher than in control plants (104–136%). No such effect was observed in over shaded (90%) and under shaded (10%) plants.

The growth of winter buds affects the yield of new shoots in spring. Buds with greater size and leaf number give a better yield of new shoots. Therefore, the effect of shading on winter bud formation was investigated. Table 2 shows that shading did not affect the growth of winter buds irrespective of shading period. Similar results were obtained from experiments where the shading ratio was changed with the exception that considerable abscission of overwintering leaves was observed in 90% shaded plants.

The yield of new shoots in the first flush of tea was measured at the stage of three leaves and a bud (Fig. 7). Yields from shaded plants were 103—137% and 126—140% of the control in Exp. A and Exp. B, respectively. Ninety % shading markedly reduced yield however due to abscission of overwintesing leaves.

To examine whether increased yield was due directly to improvement of photosynthetic rate by shading or to improvement of another condition, the relationship between increased photosnthetic rate and yield was analyzed using the results in Figs. 5-7 (Fig.8). In Exp A, both quantities were highly correlated sug-

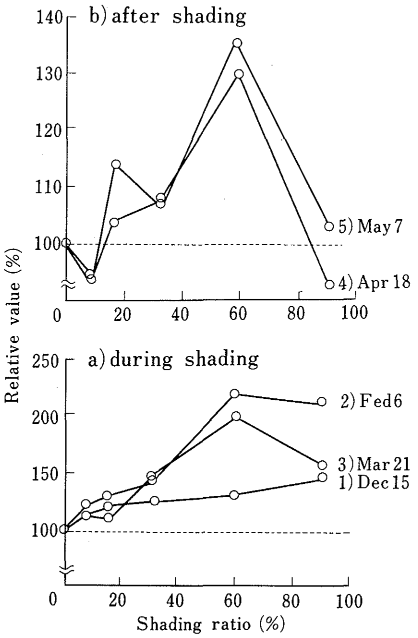


Fig. 6. Effect of shading ratio on protection from cold-induced depression of maximum photosynthetic rate (Experiments conducted according to Exp. B in Fig. 1).
Rate of photosysnthetic $O_2$ evolution of shaded leaves expressed as percentage of value for unshaded leaves. Sampling dates were as follows: 1) Dec. 15, 2) Feb. 6, 3) Mar. 21, 4) Apr. 18, 5) May 7. a, during shading treatment; b, after removal of shading. Material: cv. Yabukita.

gesting that the improvement of photosynthetic rate by shading probably caused increased yield. A similar relationship was observed for Exp B except at 8% and 90% shading. The abscission of overwintering leaves at 90% shading caused the decreased yield. In the case of 8% shading, the yield increased by about 16%, although the photosynthetic rates decreased slightly. Because there was persistent drought and low temperature in the experimental period, protection from water imbalance was probably one of the cause of increased yield.

## Discussion

Since the photosynthetic rate and colour of overwintering leaves were less damaged under shaded by other leaves (Table 1), photoinhibition might increase with increasing light intensity. Artificial shading probably retards injury to photosynthesis in overwintering leaves, and might lead to an increase in yield, since the growth of new shoots in the first flush is dependent on photosynthesis in overwintered leaves[5]. Protection from injury by shading was indeed observed (Figs. 5 and 6); photosynthesis in shaded leaves was higher than in control plants and this effect persisted even after the removal of shading. In addition, yield in the first flush of tea was increased by shading (Fig. 7).

The improvement of photosynthetic rate in overwintered leaves by shading is one possible cause for increased yield (Fig. 8). Besides protection from photoinhibition however,

Table 2. Effects of shading on growth of winter buds.

| | Plots | Oct.26 | Dec. 1 | Feb.26 | Mar.14 | Mar.28 |
|---|---|---|---|---|---|---|
| Length | Cont (no.1) | 10.0±3.8 | 10.4±2.7 | 10.6±2.6 | 12.2±2.8 | 13.7±2.9 |
| of | E- (no.2~4) | | 10.4±3.5 | 10.4±2.9 | 11.1±2.1 | 13.9±2.9 |
| shoots | L- (no.5~7) | | | 10.1±2.9 | 10.6±2.7 | 14.3±3.7 |
| (mm) | | | | | | |
| Number | Cont (no.1) | 3.9±0.7 | 4.1±0.8 | 4.7±0.5 | 4.8±0.5 | 4.7±0.6 |
| of | E- (no.2~4) | | 4.0±0.9 | 4.7±0.6 | 4.7±0.7 | 4.5±0.5 |
| leaf | L- (no.5~7) | | | 4.7±0.6 | 4.4±0.7 | 4.7±0.6 |
| intials | | | | | | |

For plots, see Exp. A in Fig. 1.
Standard deviations are shown for all data.
Material: cv. Yabukita.

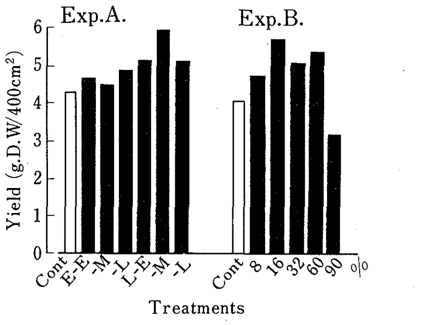


Fig. 7. Effect of shading on yield in first flush of tea. For symbols in Exp. A and Exp. B, see plots in Fig. 1.

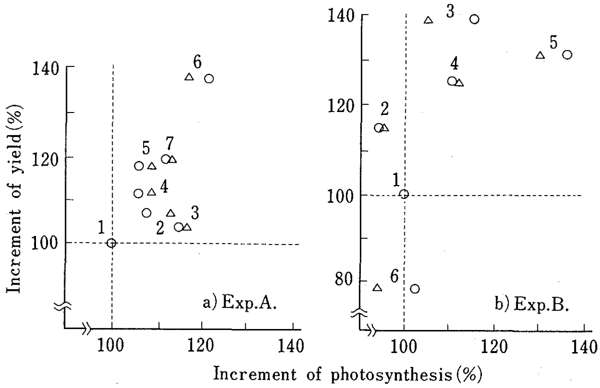


Fig. 8. Relationship between increases in photosynthetic rate and yield induced by shading.
Data obtained from Exp. A (a) and Exp. B (b) of Figs. 5—7, and expressed as percentages of values for unshaded leaves. Yield measured on Apr. 28 (Exp. A) and May 8 (Exp. B). Maximum rates of photosynthetic $O_2$ evolution measured on Apr. 12 and Apr. 25 (Exp. A) and Apr. 18 and May 7 (Exp. B).Numbers correspond to the respective plot numbers in Exps. A and B in Fig.1.

shading might increase the temperature of air surrounding overwintering leaves at night and reduce the daytime temperature[11] thus reducing excessive transpiration in overwintering leaves[11]. In this experiment, the temperature of air surrounding overwintering leaves at night increased about 0.5—1.0℃ at Feburuary by 60% shading (data not shown). But cold injury induced by freezing per se scarcely occurrs in tea plants. One of the cold injury, the green withering of tea leaves, is induced by obstruction of water supply, that is by excess transpiration and freezing of the trunk or soil. The green withering of tea leaves suppressed the growth of new shoots in the first flush of tea. Shading might improve the water conditon of tea plants resulting in an increased yield in the first flush of tea. The fact that the increase in yield in Exp. B was higher than in Exp. A (Fig. 8) was probably due to the improvement of water condition as well as the improvement of photosynthetic rate by shading. In addition, the reduction of day temperature by shading might induce cold acclimation, and tea plants might thus avoid the cold injury in late-autumn. Although the time of shading did not markedly influence the yield in Exp. A (Fig. 7), protection from cold injury might also contribute to incresed yield.

## Summary

The interaction of light and low temperature in the depression of photosynthesis in tea leaves was investigated. The photosythetic rate was higher in overwintering leaves which had been shaded by other leaves than in unshaded leaves (Table 1). When leaf discs or single leaves were chilled at 12℃ in light (12 klx) for two days, the photosynthetic rate and the light saturated Hill activity were depressed to about 60% of the control value. These depressions were reduced by shading 25% of the full light intensity (Fig. 2). When field-grown tea plants were shaded using lawn cloth during winter, the photosynthetic rate of overwintering leaves was also higher than in control plants (Fig. 4). These results indicate that cold-induced depression of photosynthesis in overwintering tea leaves is probably a consequence of photoinhibition.

The above results suggest that artificial shading can ameliorate cold-induced depression of photosynthesis in overwintering tea leaves. The photosynthetic rates of overwintered leaves were indeed higher during and after shading using lawn cloth, resulting in an increased yield in the first flush (Figs. 5—7).

## Acknoledgement

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* In Japanese with English summary.
** In Japanese

〔和 文 摘 要〕

## チャ葉の光合成阻害における光と低温の相互作用

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チャ葉の光合成阻害における光と低温の相互作用について検討した．他の葉で遮断されている越冬葉の光合成速度は遮蔽されていない葉よりも高く（第1表），低温阻害に光強度が関係することが予想された．そこで，葉ディスクまたは個葉を用いて明下（12 klx），12℃ の低温処理を2日間行なうと，光合成速度と光飽和のヒル反応活性はともに対照（20℃）の 60% に低下した．そのとき，光強度を 25% 遮光すると，これらの低下の程度は小さかった(第2図)．また，ほ場で生育している茶樹を冬季間，寒冷紗で遮光しても，光合成速度は高い値で推移した(第4図)．これらの結果から，チャ越冬葉の光合成低温阻害は光障害により起きることが示唆された．

以上の結果は人為的な遮光処理によりチャ越冬葉の光合成低温阻害を軽減できることを示唆している．実際，寒冷紗による遮光で越冬葉の光合成は遮光期間中も除去した後も高く保たれ，一番茶の収量の増加も認められた（第5～7図）．