Varietal Differences and Effects of Nitrogen Fertilization on Decline of Photosynthetic Rate in Overwintered Tea Leaves*

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In overwintered tea leaves, photosynthetic rate irreversibly decreased even after the plucking of new shoots due to senescence³⁾. THOMAS and STODDART⁸⁾ showed in their review that the process of leaf senescence is genetically controlled and programmed. Recently it was reported that the rate of senescence was different among isolines and genetically influenced in maize⁴⁾. It has been recognized in tea plants¹⁾ that the rate of dark-induced senescence is different among cultivars. Thus, differences in the decline of photosynthesis among cultivars were investigated in overwintered leaves to determine whether or not photosynthesis is affected by genetic control of leaf senescence.

Genetic control of leaf senescence is influenced by environmental and external factors. Competition for untrients among organs, for example, seems to induce senescence; MEI and THIMANN⁷⁾ showed that foliar nitrogen deficiency is part of the senescence syndrome. In tea plants, although photosynthetic rate is enhanced by nitrogen fertilization⁶⁾, the effect of fertilization on senescence has not been established. This study was undertaken to clarify the effects of nitrogen fertilization on senescence in overwintered tea leaves.

Materials and Methods

Exp. 1. Differences among various cultivars of tea in irreversible decline of photosynthesis in overwintered leaves

Mature tea plants (*Camellia sinensis* (L.) O. Kuntze) were used and experiments were repeated over three years. Eight year-old plants (cvs. Yabukita, Kanayamidori,

Okuyutaka, Surugawase, Yamatomidori and Asatsuyu), 22 year-old mature plants (cvs. Yabukita, Kanayamidori, Fujimidori, Surugawase, Yamatomidori, Asatsuyu and Tamamidori) and 3 year-old plants (cvs. Yabukita, Okuyutaka, Yamatomidori and Asatsuyu) were used.

Exp. 2. Effect of nitrogen fertilization on irreversible decline of photosynthesis in overwintered leaves

One year-old developed cutting tea plants (cv. Yabukita) grown in nursery beds were used. In one experiment, ammonium sulfate (28.4kg/10are) was applied on Mar. 15 and 31. Bud opening was on Apr. 8. New shoots were removed on Apr. 28. In another experiment, ammonium sulfate (28.4 kg/10are) was applied on Mar. 26 and Apr. 7 (early-N), or May. 7 and 14 (late-N). New shoots were removed on May 10.

Measurement of photosynthetic rate and cellular components

Maximum photosynthetic rate was measured as described previously with an oxygen electrode method²⁾. Contents of soluble protein and fraction-I protein were measured as described previously³⁾.

Results

Exp. 1. Differences among various cultivars of tea in irreversible decline of photosynthesis in overwintered leaves

To understand the role of genetic factor(s) in the irreversible decline of photosynthesis, differences among various cultivars of tea were investigated. In this work, high yield cultivars (cvs. Yabukita, Kanayamidori, Okuyutaka and Fujimidori) and other cultivars (cvs. Yamatomidori, Asatsuyu, Surugawase and Tamamidori) were used. To minimize the effects of environmental factors, experiments were carried out over three years using plants

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Fig. 1. Differences among various cultivars in irreversible decline of photosynthesis in overwintered tea leaves.

a, Change in photosynthetic rate of overwintered leaves in 8 year-old plants.

b, Relative rates of photosynthesis as a function of developing leaf number. Number of leaves on new shoots in various cultivars was measured every 5 days. Values as percentages of maximum rates of photosynthesis are expressed as a function of leaf number in new shoots.

○, Yabukita; ●, Kanayamidori; □, Okuyutaka; ×, Surugawase; △, Yamatomidori; ◐, Asatsuyu.

of different age.

Fig. 1 shows results obtained with 8 year-old plants. Similar results were obtained with 3 and 22 year-old plants. Photosynthetic rates were maximum at the time of bud opening and decreased with the development of new shoots (Fig. 1a). Photosynthetic rates were higher in high yield cultivars than in low yield ones. The time of bud opening and the growth rate of new shoots differed between cultivars. To minimize the effect of the age of new shoots, the decline in photosynthetic rate was expressed as a function of developing leaf number (Fig. 1b). Photosynthetic rates in Asatsuyu and Yamatomidori declined faster than in Yabukita and Okuyutaka. Kanayamidori and Surugawase showed an intermediate rate of decline of photosynthetic rate. In Table 1, the rates of photosynthesis at the time when new shoots had developed four leaves are compared with the respective maximum rates. It is clear that the decline in high yield cultivars was slower than in others, irrespective of measurement time and plant age. These results suggest that the irreversible decline in photosynthesis is influenced genetically.

Exp. 2 Effect of nitrogen fertilization on irreversible decline of photosynthesis in overwintered leaves.

Fig. 2 shows the effect of nitrogen fertilization on photosynthesis in overwintered leaves.

Table 1. Differences among various cultivars in the decrease of maximum photosynthetic rate in overwintered tea leaves.

Cultivars	Relative value of photosynthetic rate (%) [*]		
	3 years-old	8 years-old	22 years-old ^{**}
Yabukita	91	88	94
Kanayamidori		79	89
Okuyutaka	89	84	
Fujimidori			98
Yamatomidori	80	71	76
Asatsuyu	70	69	70
Surugawase		76	86
Tamamidori			88

^{*}Photosynthetic rates when new shoots had developed four leaves were compared with maximum rates.

^{**}Age after plants were transferred to field. Photosynthetic rates for each plant were measured in different years.

The photosynthetic rate in control leaves sharply increased up to bud opening on Apr. 8. This increase is due to recovery from chilling injury. Thereafter it gradually decreased and this decrease continued after the removal of new shoots on Apr. 28. When ammonium sulfate was applied on Mar. 15 and 31, the photosynthetic rate was enhanced to 115–125% of the control value until bud opening. However, it decreased after bud opening and this decrease continued even after the plucking of new shoots. Moreover, the decrease was faster than the control value and the photosynthetic rate finally reached the same level as that of the control.

Fig. 3 shows relative values for the photosynthetic rate and the contents of fraction-1 protein and soluble protein. In this experiment, ammonium sulfate was applied on Mar. 28 and Apr. 7 (early-N), or May 7 and 14 (late-N). In early-N plants, all three parameters were enhanced. Some enhancement was also observed in late-May unlike the results in Fig. 2. In this experiment, apical buds were damaged by cold nights between Mar. 25–29 and axillary buds resumed growth around Apr. 20. Therefore, that all

three parameters maintained high values may be due to the fact that the growth of new shoots was delayed by more than 2 weeks. In late-N plants, the effect of nitrogen fertilization on soluble protein was apparent but the effect was not so clearly seen in the case of photosynthetic rate and fraction-1 protein, where only 5–8% enhancements were observed. These results indicate that although nitrogen fertilization can enhance photosynthetic rate, it cannot delay senescence. Moreover, nitrogen fertilization, when applied after bud opening, does not effectively enhance the photosynthetic rate.

Discussion

The process of leaf senescence seems to be controlled genetically since rates of senescence differed among cultivars^{4,8}. In tea plants, it has been recognized that dark-induced senescence differs among cultivars: decrease in photosynthesis is less in Kanayamidori than in Asatsuyu¹. In this work (Fig. 1), the irreversible decline of photosynthesis was less in cvs. Yabukita, Kanayamidori, Okuyutaka and Fujimidori than in the other four cultivars. This relationship was recognisable in plants of different age over a period of at least three years (Table 1). In addition, since the decline was not influenced by the plucking of new shoots³ or by the application of nitrogen (Fig. 2), this process seems to be tightly programmed.

It is interesting that photosynthetic rate, the rate of senescence and yield seem to be related to each other; cultivars having a high photosynthetic rate and a slow rate of senescence give high yield. These results support the finding⁵ that the growth of new shoots in the first flush depends on photosynthesis rather than carbohydrate stored in the previous autumn and winter. Since overwintered leaves are considered to influence the growth of new shoots in the second flush as well as in the first flush, further understanding of the mechanism of the irreversible decline and the cause of differences among cultivars is necessary.

It has been shown that photosynthetic rate is enhanced by nitrogen fertilization in tea plants⁶. The effect of nitrogen fertilization on senescence has been unclear, however. The present study showed that the photosynthetic

Fig. 2. Effect of nitrogen fertilization on irreversible decline of maximum photosynthetic rate in overwintered leaves.

Ammonium sulfate (28.4 kg/10 are) was applied (●) on Mar. 15 and 31, or not (○). Bud opening was on Apr. 8 and new shoots were removed on Apr. 28.

Fig. 3. Effect of time of nitrogen fertilization on maximum photosynthetic rate and contents of soluble protein and fraction-1 protein in overwintered leaves.

Ammonium sulfate (28.4 kg/10 are) was applied on Mar. 26 and Apr. 7 (solid lines, early-N plant), or on May 7 and 14 (dotted lines, late-N plant). In both cases, new shoots were removed on May 10. a, maximum rate of photosynthesis; b, content of soluble protein; c, content of fraction-1 protein. Values are expressed relative to those of unfertilized plants.

rate in overwintered leaves was enhanced but the onset of senescence was not delayed by nitrogen fertilization (Fig. 2).

The enhancement of photosynthetic rate was small when nitrogen was applied after bud opening (Fig. 3). The photosynthetic rate after plucking new shoots was highly correlated with the content of fraction-1 protein in overwintered leaves. However, the biosynthesis of fraction-1 protein was not enhanced by nitrogen fertilization. This may be one of the reasons why nitrogen fertilization was ineffective in enhancing photosynthesis. Although changes in protease activity do not correlate with changes in photosynthesis in overwintered tea leaves during senescence¹⁰, a protease specific for RuBPCase^{9,11} might be involved in the degradation of fraction-1 protein. Alternatively, since it has been reported^{9,11} that these proteases are localized in vacuoles and separated from RuBPCase, interactions between vacuoles and chloroplasts might be significant in leaf senescence. However, since the biosynthesis of fraction-1 protein was observed before but not after bud opening (Fig. 3), it would be also interesting to investigate the effect of senescence on the rate of biosynthesis of fraction-1 protein in overwintered leaves.

Summary

The decline in photosynthesis of the overwintered tea leaves induced by the development of new shoots differed among cultivars of tea. The photosynthetic rate in cvs. Yabukita, Okuyutaka, Fujimidori and Kanayamidori declined less in cvs. Asatsuyu, Yamatomidori, Tamamidori and Surugawase (Fig. 1). Differences were observed between plants with different ages over a period of at least three years (Table 1). This suggests that photosynthetic decline is probably programmed genetically. In addition, since the former group have higher yields and growth rates, the extent of photosynthetic decline may be related to yield and growth.

Ammonium sulfate (28.4 kg/10 are) was applied before bud opening and changes in the photosynthetic rate of overwintered leaves were measured (Fig. 2). Although the photosynthetic rate temporarily increased to 115–125% of the control, it gradually declined to the control level. In another experiment, ammonium sulfate was applied before and after bud opening (early-N and late-N, respectively) (Fig. 3). The photosynthetic rate and contents of soluble protein and fraction-1 protein increased to 110–120% of the control

with early-N, while with late-N, the content of soluble protein increased by 5–18%, and the photosynthetic rate and content of fraction-1 protein increased by only 6–8%. These results indicate that nitrogen fertilization can enhance photosynthetic rate but not delay senescence.

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〔和 文 摘 要〕

茶越冬葉の光合成低下の品種間差異と窒素施肥の影響

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新芽生育に伴う越冬葉の光合成低下は品種により異なり、あさつゆ、やまとみどり、たまみどり、するがわせに比べてやぶきた、おくゆたか、ふじみどり、およびかなやみどりの光合成低下は小さかった(第1図)。この品種間差異は異なる樹令の茶樹で3年間、認められており(第1表)、光合成低下は遺伝的に支配されていると予想された。また、後者の4品種は高い収量と生育を示す品種であり、光合成の低下程度と収量、生育との関連が考えられた。

硫安(28.4kg/10a)を萌芽前に施肥したところ(第2図)、越冬葉の光合成速度は一時的に無施肥の115–125%に増加したが、時期の経過に伴ない無施肥と同程度に低下した。また、硫安を萌芽前と萌芽後に時期を変えて施肥すると(第3図)、萌芽前施肥では光合成速度、可溶性タンパク質、フラクシオン-1タンパク質ともに無施肥の110–120%に増加した。一方、萌芽後施肥では可溶性タンパク質の増加は5–18%であったが、光合成速度とフラクシオン-1タンパク質は6–8%増加しただけであった。以上の結果から、窒素施肥は光合成速度を増加させるが、老化を遅らせることはできないことがわかった。