

Comparison of the Effect of Shading on
Dry Matter Production and Fruits Yield in Strawberry
(*Fragaria × ananassa* Duch.) Cultivars
‘Mouikko’ and ‘Tochiotome’

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イチゴ促成栽培における遮光の有無が
イチゴ品種‘もういっこ’と‘とちおとめ’の
乾物生産と収量に及ぼす影響

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I Introduction

Strawberry (*Fragaria × ananassa*) exports from Japan has been increased from 73 t in 2007 to 526 t in 2016 (alic trend report, 2017), and it is becoming increasingly important to develop methods of stable high-level production in order to meet both domestic and foreign demand. In view of the changes in the global demand for strawberries, we are trying to breed new cultivars and increase the use of environmental control technologies. To date, a number of high-yield cultivars have been bred in Japan, for example ‘Benihoppe’ in Shizuoka prefecture in 2002, ‘Yuubeni’ in Kumamoto prefecture in 2015, and ‘Mouikko’ in Miyagi prefecture in 2008. In order to fully exploit high-yielding cultivars through environmental control, it is necessary to clarify the plants response characteristics to the environment. Mochizuki et al.

(2013) analyzed ‘Benihoppe’ in detail, clarifying the growth characteristics of this high-yielding cultivar. Since there has been no reports about responses to the environment of high-yield cultivars, further investigation is required to optimize cultivation and environmental control.

Plants require light for proper growth and development. It has been reported that total dry matter (TDM) is significantly correlated with the fraction of incident light interception. Kaneko et al. (2015) reported a linear relationship between biomass production and intercepted light in low-truss cultivation of tomato irrespective of the growth stage at transplanting. Higashide and Heuvelink (2009) observed that the TDM was higher in modern tomato cultivars than in old cultivars because modern cultivars received more light. In the case of rice plants, TDM increases as the amount

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of received light increases because the leaves stand more upright (Sakamoto et al., 2006). This relationship has also been reported in cotton plants (Bai et al., 2016). These results suggest that the amount of light intercepted by plant canopy plays is important in determining plant biomass production and growth.

The amount of intercepted light by a plant is estimated based on the use of the leaf area index (LAI) and the light extinction coefficient, and is affected by the size and number of leaves and by their three-dimensional distribution. This means that plant acclimation to environmental change is important in considering the amount of light intercepted. It is well known that leaf morphology is very plastic and plants are usually dynamically acclimating to their environment, including the lighting conditions (Duursma et al., 2012). For instance, the total leaf area of rice plants grown under low light is larger than in plants grown under high light conditions (Makino et al., 1997). According to the results from growth analysis, such changes are associated with the preferential investment of resources. This result suggests that changes in the distribution of resources such as nitrogen and dry matter are important for environmental adaptation. Additionally, when two different cultivars of *Spiraea alba* (meadowsweet) were grown under conditions of 50% shade, the degree of change in leaf greenness was different depending on the cultivar (Liu and Su, 2016). These results indicate that crop plants respond to shading by changing not only the biomass allocation at the level of the whole plant but also the morphology of individual leaves. On the other hand, there have been few quantitative analyses of the relationship between changes in whole-plant growth and morphological changes, for instance, changes in dry matter allocation, or total leaf area. Mochizuki et al. (2017) reported that a decrease in solar radiation leads to a decrease in fresh fruit yield and the appearance of non-marketable fruits. However, the mechanism behind the decrease in fruit yield has not been fully analyzed in relation to either dry matter production or the allocation of dry matter at whole plant level. In addition, little is known about the environmental responses of high-yield varieties.

Our aim in this study was to evaluate the relationship between morphological change and the biomass production of strawberry plants grown under shaded conditions. In particular, we focused not only on changes in total leaf area but also on the alteration of biomass allocation at the

whole-plant level. The adaptation strategies in two different strawberry cultivars were assessed in this study.

II Materials and methods

1. Plant material and cultivation

Two cultivars were used for the experiments: 'Mouikko', which has been the standard cultivar for farmers in Miyagi prefecture for many years; and 'Tochiotome' which is the most popular cultivar in Japan and famous for its high production volume. The experimental period was 6 months from October 5, 2015 to the end of April, 2016.

Plants were grown by forcing culture in the greenhouse at GRA Co., Ltd., Miyagi, Japan. Runner plants were lifted in the field in early July 2015 and rooted in a greenhouse at around 20°C under natural light conditions. When rooted, these plants were potted into plug trays using a peat-based potting compost, and grown under the same greenhouse conditions before transplanting. The mean number of unfolded leaves at this point was 3.0 ± 0.5 for both cultivars. In the middle of September, young plants were transferred to polyethylene pots (11 cm diameter \times 13 cm depth; 1.2 L volume), and river sand was used as the soil substrate. Plants were set 15 cm apart in rows and with rows 25 cm apart. All plants were fertilized with Otsuka-A nutrient solution (Otsuka Agri Techno Co. Ltd., Osaka, Japan; consisting of 8.8 mM NO₃, 5.1 mM K⁺, 4.1 mM Ca²⁺, 1.5 mM Mg²⁺, 0.7 mM H₂PO₄, 3 mg L⁻¹ iron, 0.05 mg L⁻¹ manganese, 0.5 mg L⁻¹ boron, 0.05 mg L⁻¹ zinc, 0.02 mg L⁻¹ copper, and 0.01 mg L⁻¹ molybdenum) adjusted to an electrical conductivity (EC) of 0.7 mS cm⁻¹ and pH 6.0. The supply of nutrient solution was controlled by a time switch that released 50 ml of solution at 09:00, 12:00, and 14:00. The nutrient solution was supplied with a drip irrigation system. The field experiment was a randomized block design with two replicates, each with 60 plants of each cultivar. Fruit yield was calculated using 10 plants selected from the 60 for each cultivar. At the start of the experiment all runners were removed and the number of leaves was the same on each plant. The petiole length of the last fully developed leaf was almost at the same level on each plant. The progress to flowering (the day of anthesis in each plant) was recorded once a week throughout the experiment. Runners were counted and removed from five plants in each plot once a week during the growing season. Both the total

number of inflorescences and the number of flowers in each plant were recorded at the end of the experiment (The number of flower buds was not determined). Plant protection was performed according to the minimum locally recommended spraying program. Fruits were harvested two to three times per week during the cultivation period. The number and weight of all berries was recorded and they were graded as marketable or non-marketable. In this study, marketable fruits were defined as fruits ≥ 7.0 g in weight, and non-marketable fruits as < 7.0 g in weight or malformed. After measuring fresh weight, the fruits were oven-dried and the dry weight was measured. Plants used in this experiment were thinned to leave 4–5 fully expanded leaves attached. The thinned leaves were also collected and measured. Temperature inside the greenhouse was controlled using heaters and coolers so that the temperature in the greenhouse was maintained at 25/10 °C (day/night). At the end of November, plastic film curtains were drawn and a heater was installed to maintain the greenhouse air temperature during the night above 10°C. The daily average temperature was 14.4 °C throughout the cultivation period, and the daytime and nighttime average temperature were 18.2 °C and 10.6 °C, respectively. Two light intensity treatments were used, untreated and the other 50% shade using polyethylene film (Dio karucool SW-50, Dio chemicals, Ltd., Japan) suspended 1.0 m above the cultivation bed. During daytime, light intensity at the canopy level under the shaded netting was maintained 50% of the light intensity of the unshaded area. Solar irradiance was checked using a light-meter (Li-200SZ, Li-COR, Lincoln, US) in the middle of day on November 20, 2015. Irradiance was 106 W m⁻² in the shading treatment and 200 W m⁻² in the unshaded. The treatments started at November 1, 2015, one month after the transplanting. The monthly solar radiation in both treatments is shown in Fig. 1.

2. Determination of total dry matter and leaf area

Five plants were sampled 1, 60, 120 and 180 days after transplanting (DAT), corresponding to October 5, December 4, February 2, and April 2, respectively. For reference, the start of flowering was November 18 in ‘Mouikko’ and November 13 in ‘Tochiotome’. First fruits were harvested on December 15 in ‘Mouikko’ and December 4 in ‘Tochiotome’. Measurement of biomass and total leaf area were performed as follows. First, we measured total leaf area using a leaf area

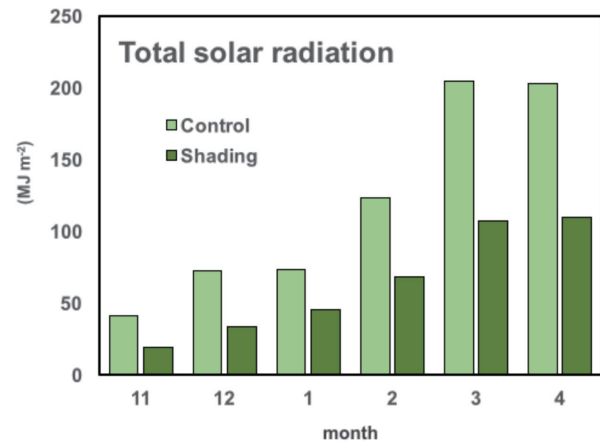


Fig 1 Monthly solar radiation inside the greenhouse during the experimental period (Nov. 2015 – Apr. 2016).

meter (Li-3100, Li-COR, Lincoln, US). Then, the plants were separated into leaves, peduncles, fruits, crowns, and roots. Especially the roots were carefully washed and the sand was removed. Finally, these organs were dried at 100°C for 72 hours with a circulation drier, and the dry weight measured after cooling to room temperature. Based on the data of TDM and total leaf area, relative growth rate (RGR), leaf area ratio (LAR), net assimilation rate (NAR), leaf weight ratio (LWR) and specific leaf area (SLA) were calculated according to the method of Saeki (1965).

3. Statistical analysis

All experimental data were subjected to analysis of variance (ANOVA) by standard procedures using R (R Development Core Team, 2013).

III Results

Fresh fruit yield was lower under the shading for both cultivars (Table 1). For ‘Mouikko’, total fruit yield under shading was 43% lower than the control, while the ratio of the fresh yield of marketable fruit to total fruit did not change between treatments. The same tendency could be seen in ‘Tochiotome’, with total fruit yield under shading 48% lower than the control. These results indicated that a reduction in the amount of light is associated with a decline in fresh fruit yield, regardless of cultivar. However, the ratio of the fresh yield of marketable fruit to total fruit decreased 26% with the shading treatment.

Table 1 Comparison of total yield, and the amount of marketable and unmarketable fruit in 'Mouikko' and 'Tochiotome' between the shading treatment and the control.

'Mouikko'			
Treatment	Total Yield (gFW plant ⁻¹)	Marketable (gFW plant ⁻¹)	Non-marketable (gFW plant ⁻¹)
Control	509.2 (100)	328.5 (100)	180.8 (100)
Shading	289.5 (57)	196.2 (60)	93.4 (52)

'Tochiotome'			
Treatment	Total Yield (gFW plant ⁻¹)	Marketable (gFW plant ⁻¹)	Non-marketable (gFW plant ⁻¹)
Control	426.8 (100)	167.2 (100)	259.7 (100)
Shading	220.1 (52)	56.3 (34)	163.7 (63)

Fig. 2 shows changes in total dry weight and total leaf area for 'Mouikko' and 'Tochiotome' at 1, 60, 120, and 180 DAT. Total dry weight was significantly decreased in shade-grown plants compared to controls at 180 DAT for both cultivars ($P < 0.05$). However, the extent of decrease in total dry weight was not the same, being 30% in 'Mouikko' and 50% in 'Tochiotome'. Thus, the degree of recovery after shading treatment varies depending on the cultivar. Total leaf area was not significantly different between the treatments in 'Mouikko' during the cultivation (Fig. 2C), neither was the number of leaves (data not shown). However, total leaf area was decreased with the shade treatment in 'Tochiotome' (Fig. 2D). Leaf area at 120 and 180 DAT was significantly

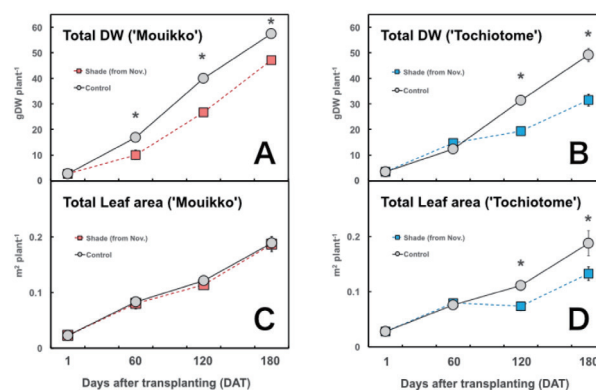


Fig 2 Changes in total dry weight and total leaf area in 'Mouikko' and 'Tochiotome' grown under shade at 1, 60, 120, and 180 days after transplanting (DAT). Error bars on each column indicate the standard error ($n = 5$). Statistical analysis was carried out between treatments using t-test. Asterisk indicates a significant difference ($P < 0.05$).

smaller in the shade treatment compared with the control. The trend observed in total leaf area showed the same tendency as for TDM in 'Tochiotome'. The number of leaves was not significantly different between treatments for 'Tochiotome' (data not shown).

Figs 3 and 4 show growth analysis results for 'Mouikko' and 'Tochiotome', calculated between days 1 and 60, days 60 and 120, and days 120 and 180. In 'Mouikko', RGR was significantly decreased in the shading treatment compared with the control between days 1 and 60, but no differences were observed in RGR between days 60 and 120 and between days 120 and 180. Thus, the decline in the final dry matter in the shade-grown plants was the result of the decrease in RGR

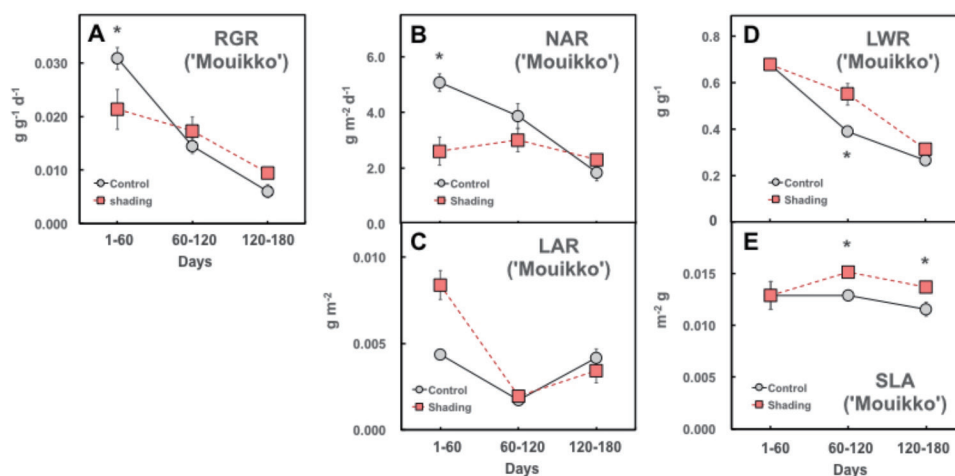


Fig 3 Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA) for plants between days 1-60, 60-120, and 120-180 in 'Mouikko'. Error bars on each column indicate the standard error ($n = 5$). Statistical analysis was carried out between treatments using t-test. Asterisk indicates a significant difference ($P < 0.05$).

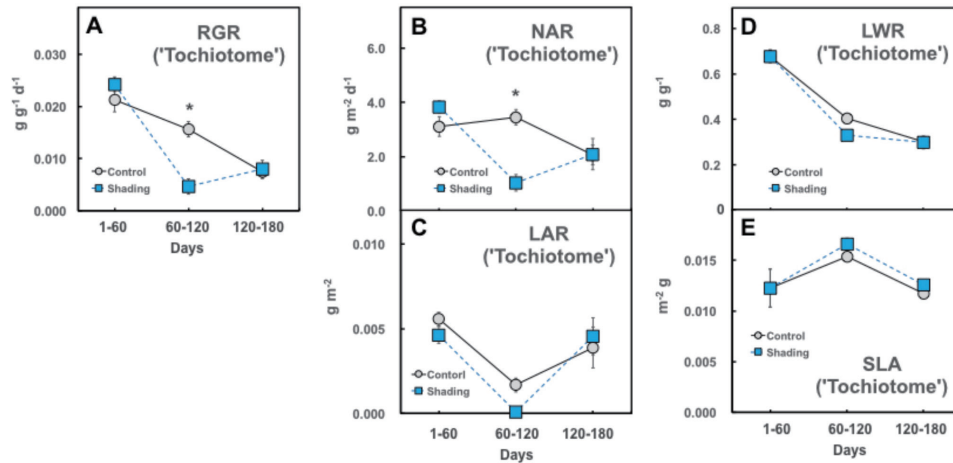


Fig 4 Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA) for plants between days 1–60, 60–120, and 120–180 in ‘Tochiotome’. Error bars on each column indicate the standard error ($n = 5$). Statistical analysis was carried out between treatments using t-test. Asterisk indicates a significant difference ($P < 0.05$).

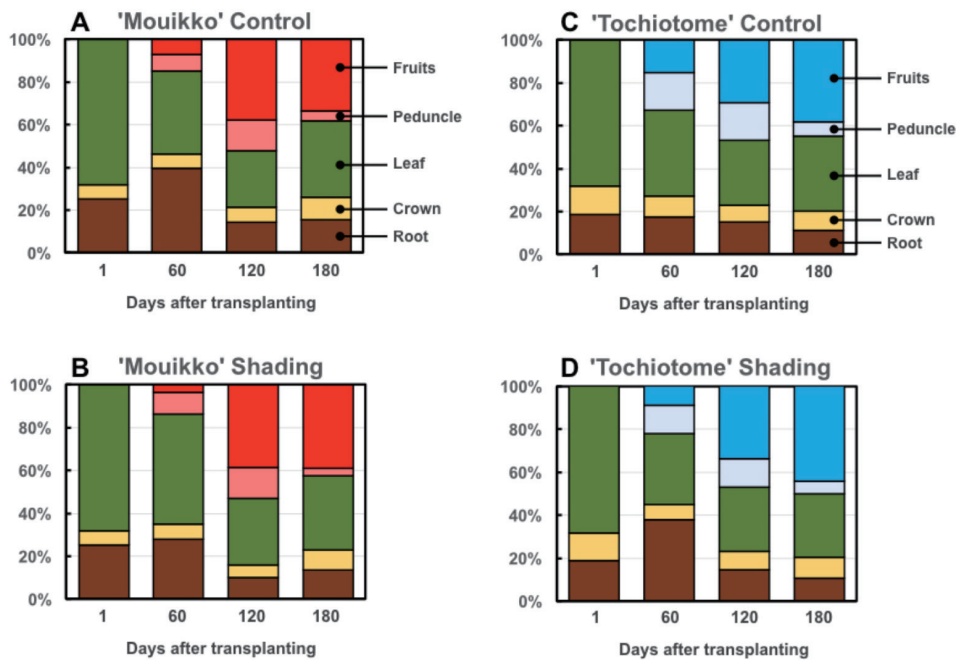


Fig 5 Biomass allocation into the fruit, peduncles, leaf, crown and roots in ‘Mouikko’ and ‘Tochiotome’ grown under shade at 1, 60, 120, and 180 days after transplanting (DAT).

during the early stage of the treatment. The smaller RGR in the shading treatment was associated with a decrease in NAR, while LAR was significantly increased between days 1–60. The changes in RGR, therefore, were mainly caused by the decline in NAR. In the case of ‘Tochiotome’, RGR showed a difference (a significant decrease in the shade treatment) only in the period of between days 60–120 (Fig. 4), explaining the decrease in TDM during the middle stage of the cultivation. In ‘Tochiotome’, there was also a decrease in NAR between 60–120 DAT. These results, indicate that the decline in RGR

between 60–120 DAT was mainly caused by the reduction in NAR. LAR is the product of LWR and SLA. LWR in ‘Mouikko’ was increased under shading between 60–120 DAT ($P < 0.05$). In addition, SLA was also higher in the shading treatment compared to controls between days 60–120 and 120–180 after transplanting. On the other hand, there were no significant differences between these values for ‘Tochiotome’. These results indicate that growth responses to the shading differ between these cultivars.

Fig. 5 shows the biomass allocation for each organ at 1,

60, 120 and 180 DAT. In ‘Mouikko’, the biomass allocation to leaf in the shading treatment was significantly higher than that in the control ($P < 0.05$) at 60 DAT, while the biomass allocation to root was significantly lower in the shading condition than in the control. In contrast, ‘Tochiotome’ doubled the biomass allocation for root under shade. The ratio of root biomass to TDM at 60 DAT was dramatically increased in the shading treatment. These results indicated that ‘Mouikko’ preferentially invested biomass in leaf, while ‘Tochiotome’ invested biomass in root under the shading conditions.

The differences in dry matter allocation are clearly reflected in the changes in the shoot /root (S/R) ratio (Fig.6). There were significant differences in the S/R ratio at 60 DAT and 120 DAT in ‘Mouikko’, with the ratio always higher in the shading treatment than in the control. However, the changes in the S/R ratio in ‘Tochiotome’ were not the same as in ‘Mouikko’. There was a significant difference in the S/R ratio at 60 DAT between the treatments in ‘Tochiotome’. These differences were thought to be due to changes in the distribution of dry matter under the shading condition.

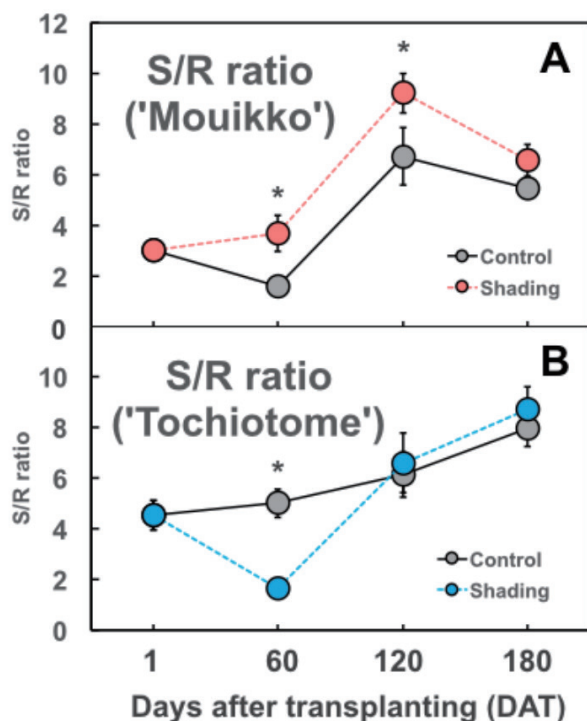


Fig 6 Changes in the shoot/root (S/R) ratio in ‘Mouikko’ and ‘Tochiotome’ grown under shade at 1, 60, 120, and 180 days after transplanting (DAT). Error bars on each column indicate the standard error ($n = 5$). Statistical analysis was carried out between treatments using t-test. Asterisk indicates significant difference ($P < 0.05$).

IV Discussion

Fruit yield declined with the shading treatment in both strawberry cultivars, ‘Mouikko’ and ‘Tochiotome’, with the level of responses being the same. Results showed that the decrease in total fruit yield was associated with the total dry matter production in both cultivars. Additionally, the number of unmarketable fruits was significantly increased in the shading treatments compared to controls in both cultivars. The same phenomena have been reported by other researchers. For example, Mochizuki et al. (2017) reported that the ratio of abnormal fruits to total fruits reached a maximum of 30% in ‘Mouikko’ grown under low irradiance. Therefore, shading treatment leads to a decrease in yield through a reduction in dry matter production.

However, many differences were observed between two cultivars regarding acclimation to shading. Surprisingly, ‘Mouikko’ grown under the shading maintained total leaf area at the same level as the control throughout the cultivation period (Fig. 2C). This phenomenon was associated with changes in the biomass allocation at the level of the whole plant (Fig. 5B). At the same time, plants grown under the shading treatment reduced investment in root biomass. The proportion of root in the TDM decreased from 40% to 28% at 60 DAT. These results indicated that ‘Mouikko’ preferentially invests dry matter in the shoots as light intensity decreases; the trade-off relationships between the growth of leaf and root exists in this cultivar. A number of researchers have suggested that the changes in biomass allocation under low irradiance are accompanied by increased light harvesting efficiency. For example, Liu and Su (2016) reported that light conditions affect plant morphology and biomass allocation in *Taxus* genus. *Taxus yunnanensis* developed larger leaves under low irradiance compared with plants grown under high irradiance. Makino et al. (1997) also reported that enlargement of total leaf area under low irradiance is important for acclimation and to maintain plant growth. The enlargement of leaf area was associated with not only with an increase in dry matter distribution to shoots but also with a change in leaf thickness. In this study, ‘Mouikko’ showed an increase in SLA under the shading. SLA is an indicator of leaf thickness; an increase in SLA indicates relatively thinner leaves for the same dry matter investment. We surmised that the increment of SLA was associated with the enlargement of LAR. Thus, in

‘Mouikko’, the decrease in light intensity appeared to induce morphological change not only at the level of the whole plant but also at leaf level in order to acclimate low light intensity and harvest light more efficiently. Considering these results, ‘Mouikko’ has the potential to acclimate to low light conditions through morphological change both at whole plant and also leaf levels.

The morphological response of ‘Tochiotome’ to low irradiance was significantly different from ‘Mouikko’. This cultivar did not show an increase in leaf dry matter under shading, regardless of the decline in the amount of intercepted light. Since the biomass allocation was unchanged, RGR at whole-plant level at 1–60 DAT was not significantly different between the shading treatment and the control. From this point, there was no significant change in the ratio of leaf dry matter to whole-plant dry matter through the end of the cultivation. These results suggest that ‘Tochiotome’ does not preferentially allocate biomass to the leaf depending on whether it is shaded or not during growth.

The mechanism for the difference between ‘Mouikko’ and ‘Tochiotome’ in reallocation of dry matter is still unknown. However, there have been some reports describing a negative correlation between the increase investment of biomass to leaf and the accumulation of photosynthates in the shoot (Kanno et al., 2009). Ohashi et al. (2000) indicated that a decrease in biomass allocation to the leaf was associated with a decrease in the accumulation of carbohydrates such as starch and sucrose. Additionally, in the case of tobacco plants, an increased investment in biomass to the leaves was accompanied by a decrease in carbohydrates in the shoots (Stitt and Schultze, 1994). These results suggest that carbohydrates play an important role for changing biomass allocation at the level of the whole plant. In the case of strawberry plants, Nishizawa and Shishido (1998) reported that root dry matter increased when petals were removed, and that an increase in starch accumulation in the roots was associated with this treatment. In addition, continuous harvesting during the winter season leads to a decrease in the number of fine roots (Nishizawa and Hori, 1989). These reports suggest that strawberry roots act as a sink organ, and it can be inferred that it is important to maintain a balance between photosynthate use for growth and stock in response to environmental changes. Further investigation is needed to establish the relationship between accumulation of carbohydrates and

biomass allocation in ‘Tochiotome’.

We investigated the effect of shading on the growth and yield of strawberry plants in the forced strawberry cultivars ‘Mouikko’ and ‘Tochiotome’, finding that their adaptation strategies to lighting conditions differed. The results of the present study indicate that ‘Mouikko’ is more adaptive than ‘Tochiotome’ under the limited light conditions because the decline in dry matter production was smaller. Taking into account the changes in biomass allocation and RGR, it appeared that ‘Mouikko’ showed positive response to the shading conditions. However, ‘Tochiotome’ was unresponsive, and it is suggested that for this cultivar the changes seen in the roots may be important for acclimating to the light environment. These findings indicate that for a good management of strawberry plants we should be aware of changes not only in the aerial organs but also those underground. These days it is relatively easy to monitor and analyze changes in the appearance of shoots using a 3D sensor like the KINECT (Hamamoto et al., 2015), but technologies for continuous monitoring of underground organs are not yet well established. Recently, there has been much discussion on the topic of non-destructive analysis of roots, such as by computed tomography scanning of roots or root image analysis using artificial intelligence (Tracy et al., 2010). In consideration of this background, we need to develop better monitoring techniques that lead to better management of crop cultivars.

V Summary

We investigated the effect of shading treatment on the growth of strawberry plants using the cultivars ‘Mouikko’ and ‘Tochiotome’. Both total fruit yield and dry matter production were significantly decreased by shading compared to controls. According to growth analysis results, the decline in dry matter production was different between cultivars, with different underlying reasons. In the case of ‘Mouikko’, there was no difference in total leaf area between the treatments, but the investment of dry matter into leaf was increased in the shading treatment. These changes were considered as a positive response to the decrease in total solar radiation. The S/R ratio was also increased in ‘Tochiotome’. On the other hand, ‘Tochiotome’ did not show changes in either the allocation of dry matter or total leaf area. These results suggest that the

strategy for adaptation to shading differs between cultivars and that acclimation involves morphological change at the whole-plant level. The mechanisms behind changes in biomass allocation is still unknown, and further investigation is needed regarding the efficient use of carbohydrates for plant growth.

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和文摘要

イチゴ品種‘もういっこ’と‘とちおとめ’を用い、遮光処理が乾物生産と収量に及ぼす効果と応答の品種差について調査した。これまでに、イチゴの環境変化に対する応答には、地上部だけでなく地下部の変化が重要であることが示されている。そこで本報告では、成長解析法を試みると同時に、地上部地下部を含む個体レベルでの乾物分配の変化にも注目し調査を行った。遮光資材を用いて日射量を半分にしたところ、品種に関わらず収量と乾物生産量が減少した。この時、総葉面積および個体レベルでの乾物分配に品種間差が認められた。‘もういっこ’では、日射量が減少しても総葉面積は対照区と同じレベルに維持され、これは葉への乾物分配を増やす応答を示したためと考えられた。‘もういっこ’は、遮光処理によって地上部/地下部比が増加しており、このような個体レベルの応答は日射量の減少に対し生長速度を維持するための積極的な応答と推察された。一方、‘とちおとめ’では、遮光によって個体乾物が減少し、これは総葉面積の減少を伴っていた。また、地上部/地下部比は遮光によって一旦は減少したが、その後は対照区と同じレベルに維持され、結果として遮光により個体レベルで乾物分配が変化することはなかった。以上のことから、日射量の減少に対する応答には品種間差が存在し、遮光に対する個体としての生長戦略が異なることが示唆された。今後は、各部位への炭水化物の集積など、乾物分配の変化の理由について調査することが必要と考えられた。