INTRODUCTION

‘Misato-zairai’ is a local soybean cultivar in Mie Prefecture. Seed size is relatively large; for example, 100-seed weight of ‘Fukuyutaka’, a popular cultivar in western Japan, is 30 g and that of ‘Misato-zairai’ is 45–50 g (Nose et al., 2008; Nagasuga et al., 2011). The seeds of ‘Misato-zairai’ are commercially available in parts of Mie Prefecture; owing to their sweet taste, these seeds are used for processed foods such as tofu, soybean curd, and kinako, roasted soybean flour. However, this cultivar is difficult to grow and its seed yield is unstable (Nose et al., 2008); these drawbacks prevent ‘Misato-zairai’ from becoming the predominant cultivar grown by farmers.

Maximum seed yields of ‘Misato-zairai’ and ‘Fukuyutaka’ are similar levels, but the yield components and light intercepting characteristics differ (Nagasuga et al., 2011). As mentioned above, ‘Misato-zairai’ seeds are larger and it has fewer seeds and pods than ‘Fukuyutaka’ (Nose et al., 2008; Nagasuga et al., 2011). Because of vigorous vegetative growth, leaf area index of ‘Misato-zairai’ is often higher than that of ‘Fukuyutaka’ from the beginning of bloom stage (Nagasuga et al., 2011; Nagasuga et al., 2014). Additionally, the stem of ‘Misato-zairai’ at maturity is often heavier, and these caused lower seed-stem ratio (Nagasuga et al., 2011). In the Tokai area (central Japan), vigorous vegetative growth often results in lodging, and partial leaf thinning before the beginning of bloom stage is recommended even in ‘Fukuyutaka’ (Hayashi et al., 2008).

Restriction of vigorous vegetation is important for stable seed production, particularly in ‘Misato-zairai’. Vigorous vegetation also negatively affects canopy light interception. ‘Misato-zairai’ has dense foliage in the upper layer of the canopy (Nagasuga et al., 2011; Nagasuga et al., 2013b) and its leaf inclination angle is lower than in ‘Fukuyutaka’ (Nagasuga et al., 2011; Nagasuga et al., 2013a). However the two cultivars do not differ significantly in the light interception coefficient, an indicator of canopy light interception (Nagasuga et al., 2011; Nagasuga et al., 2013b). These observations suggest that unstable seed production of ‘Misato-zairai’ results from its inferior utilization of light energy for leaf photosynthesis, of photosynthates for seed production, or both.

We have previously measured seed weight and yield components stratified by 10-cm intervals above the ground and their correlation with relative light intensity for the leaflets elongated from each layer at the beginning of seed development in these two cultivars (Nagasuga et al., 2019). Seed weight per node number was greater in higher layers (brighter light), and there was a significant linear relationship between seed weight per node number and relative light intensity in ‘Fukuyutaka’. A similar tendency was found in ‘Misato-zairai’, but the regression was logarithmic and the increase in seed weight per node number was small at high relative light intensity. We concluded that light utilization for seed production of ‘Misato-zairai’ is inferior to that of ‘Fukuyutaka’, particularly at high light intensity.

In soybean, both vegetative and reproductive growth continue after the beginning of bloom stage. Japanese soybean cultivars are determinate, so the growth of shoot apices on the main stem finishes after the beginning of bloom stage. Yet, branching continues; as a result, pod growth...
competes with branching for photosynthates. Branching is vigorous in ‘Misato-zairai’ (Nagasuga et al., 2011), so utilization of photosynthates for branching might decrease that for pod and seed growth even though leaves can easily use light energy for photosynthesis. As the photosynthetic rate of ‘Misato-zairai’ leaves under wet soil conditions is similar to that of ‘Fukuyutaka’ (Hattori et al., 2019), lower light utilization in seed production might be associated with vigorous branching.

In this study, to compare light utilization by ‘Fukuyutaka’ and ‘Misato-zairai’ plants, we exposed them to various levels of shading. To examine a simple sink-source relationship between pods and leaves only, we removed shoot apices on the main stem, branches, and new lateral buds. Plants were shaded from the beginning of bloom stage to maturity because dry matter accumulation dependent on light intensity during the reproductive stage has a greater impact on seed production than that during the vegetative stage (Kumudini, 2002).

MATERIALS AND METHODS

Plant materials

Experiments were performed from 2010 to 2012 at the Farm Station, Mis University (34°81′N, 136°27′E). The seeds of ‘Fukuyutaka’ and ‘Misato-zairai’ were sown on 27 July 2010, 25 July 2011, and 3 August 2012 in rows 0.7 m apart at a spacing of 0.2 m between plants (7.14 plants m⁻²). Four seeds were placed in a 5-cm-deep hole and covered with adjacent soil by hand. After establishment (2 weeks after emergence), seedlings were thinned to one per hill. In each year, basal fertilizer (9 g N m⁻², 30 g P₂O₅ m⁻², 30 g K₂O m⁻²) and 30 g m⁻² garden lime were mixed into the soil before sowing.

Shading treatment

Shading treatment was applied to 2.8×3.0 m areas from the beginning of bloom stage (9 Sep. 2010, 8 Sep. 2011 and 8 Sep. 2012). A steel frame (1.5 m high) whose top and all sides were covered with one layer of white cheesecloth (light shading, S1), one layer of white and one of black cheesecloth (moderate shading, S2), or three layers of black cheesecloth (heavy shading, S3), was placed above the plants. Sunlight was reduced by 14% in S1, by 48% in S2, and by 89% in S3. Control plots were not shaded. The experiments used a split-plot design with two replications; each block was 1.4 m². The main plot had three shading treatments, and the split plot had two cultivars.

Measurements

Plants (10 per cultivar) were harvested from each treatment at maturity: on 8 Nov. (S2 and S3 in ‘Fukuyutaka’), 9 Nov. (control and S1 in ‘Fukuyutaka’ and ‘Misato-zairai’) and 12 Nov. (S2 and S3 in ‘Misato-zairai’) in 2010, 9 Nov. (all treatments in both cultivars) in 2011, and 6 Nov. (control and S1 in ‘Fukuyutaka’), 8 Nov. (S2 and S3 in ‘Fukuyutaka’), 9 Nov. (control and S1 in ‘Misato-zairai’), or 12 Nov. (S2 and S3 in ‘Misato-zairai’) in 2012. Samples were air-dried completely (to constant weight), separated into seeds, pods and stems, and weighed. Seed distribution was calculated as the ratio of seed weight to total weight (seeds, pods, and stems). To simplify the sink-source relationship to that between pods and leaves only, we removed shoot apices from the main stem, branches, and all lateral buds continuously during the treatments. Tukey-Kramer multiple range test was performed with Excel.

RESULTS

Monthly mean air temperature from July to November (Table 1) was moderate in the 3 years. Monthly sunlight duration (Table 1) was longer than 30-year mean values in the 3 years; the cumulative sunlight duration from September to October (growth period during shading) was 320 hours in 2010, 340 hours in 2011, and 395 hours in 2012. Light shading did not significantly decrease seed weight, which was sometimes higher than in the control in ‘Misato-zairai’ (Fig. 1A and E). However moderate (except for ‘Misato-zairai’ in 2010 and 2011) and heavy shading decreased seed weight in both cultivars (Fig. 1A and E). Pod number (Fig. 1B and F) and seed number (Fig. 1C and G) were decreased or tended to be decreased by moderate shading, and were decreased by heavy shading. Heavy shading decreased 100-seed weight in 2010 and 2012, and control did not show the highest 100-seed weight in 2011 and 2012 in both cultivars (Fig. 1D and H). In ‘Misato-zairai’, 100-seed weight in 2010 was higher than those of the other years (Fig. 1H). Total weight was decreased by moderate shading (except for ‘Fukuyutaka’ in 2012 and ‘Misato-zairai’ in 2011) and by heavy shading in both cultivars (Fig. 2A and C). Seed distribution was not affected clearly by shading, but ‘Misato-zairai’ showed lower seed distribution in 2012. Seed weight and pod number were significantly positively correlated in both cultivars (Fig. 3). Pod number and total weight were also significantly positively correlated; the slope of the regression line was steeper in ‘Fukuyutaka’ (Fig. 4). In both cultivars, 100-seed weight and seed distribution were significantly positively correlated (Fig. 5).

DISCUSSION

Although many studies have used shading to examine light utilization in soybean seed production (Mathew et al., 2000; Kakiuchi and Kobata, 2004; Liu et al., 2006; Egli, 2010), the reported results might have been affected by the fact that both pods and lateral buds grow after the begin-

Table 1 Monthly mean air temperature and sunlight duration during 2010 to 2012, and comparison with the 30-year mean values (Mean).

| Month | Air temperature (°C) | Sunlight duration (hr) |
|-------|----------------------|------------------------|
|       | 2010 | 2011 | 2012 | Mean | 2010 | 2011 | 2012 | Mean |
| July  | 27.6 | 27.2 | 27.1 | 26.3 | 200 | 191 | 210 | 189 |
| Aug.  | 29.1 | 28.0 | 28.3 | 27.5 | 256 | 194 | 249 | 215 |
| Sep.  | 26.0 | 24.6 | 25.6 | 24.0 | 201 | 173 | 180 | 169 |
| Oct.  | 19.4 | 18.7 | 19.1 | 18.3 | 119 | 167 | 215 | 165 |
| Nov.  | 12.5 | 14.5 | 12.0 | 12.7 | 197 | 145 | 154 | 163 |
In ‘Misato-zairai’, vigorous vegetative growth continues after the beginning of bloom stage (Nagasuga et al., 2011; Nagasuga et al., 2014) and might decreases seed production. In this study, we removed shoot apices, branches, and lateral buds before shading to evaluate the response of seed production to light intensity in a simple sink-source relationship between pods and leaves. Seed weight of both cultivars was decreased significantly by moderate (except for ‘Misato-zairai’ in 2010 and 2011) and heavy shading (Fig. 1), and similar tendencies were found in pod number, seed number, and total weight (Fig. 2). Pod number is an important factor that determines soybean seed yield (Board and Kahlon, 2010); the numbers of pods and seeds at the full seed stage (Board and Tang, 1995) are affected by environmental conditions such as light intensity from the beginning of bloom stage to the beginning of seed stage (Board and Kahlon, 2010). In this study, shading during the reproductive stage (including the above stages) also decreased the pod number in both cultivars (Fig. 1), and there was a significant correlation between pod number and seed weight in both cultivars (Fig. 3). Thus, the response of seed weight to shading during the reproductive stage depended more on that of pod number.

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**Fig. 1** Seed weight (A, E), pod number (B, F), seed number (C, G) and 100-seed weight (D, H) in ‘Fukuyutaka’ (A, B, C, D) and ‘Misato-zairai’ (E, F, G, H) from 2010 to 2012. Data are mean ± S.E. (n = 10). Bars with the same letters within the same year are not significantly different by Tukey-Kramer multiple range test (P <0.05).

- **Control**
- **S1**
- **S2**
- **S3**
Pod and seed numbers got higher from 2010 to 2012 in 'Fukuyutaka'; similar tendencies were found in 'Misato-zairai', but seed number of S1 was higher in 2011 than in 2012 (Fig. 1). The cumulative sunlight duration from September to October (this period corresponded to beginning of bloom to beginning of maturity) was the highest in 2012 and lowest in 2010 (Table 1); this difference agreed with the differences in pod number and total weight among the 3 years (Figs. 1 and 2). Pod number was also correlated with total weight in both cultivars (Fig. 4). Total weight can be regarded as a result of total plant photosynthesis during the entire growth period. Since all plants were cultivated under the same conditions before treatment, the difference in total weight among the treatments should result from the effect of treatment. Quantitative growth should finish before the beginning of maturity stage, these indicate that the pod number of both cultivars depended on light conditions from the beginning of bloom to the beginning of maturity stage.

Seed distribution and 100-seed weight were not reproducibly sensitive to shading (Fig. 2), and there was a significant correlation between them in both cultivars (Fig. 5). Board and Kahlon (2010) reported that shading treatment from the full seed stage to the beginning of maturity stage decreased 100-seed weight, but other study (Mathew et al., 2000) indicated that long-term shading during the reproductive stage has little effect. Both 100-seed weight and seed distribution might compete with pod and seed numbers for photosynthates and other nutrients in the absence of shading during the reproductive stage.
EFFECT OF SHADE ON SOYBEAN

Yield components responded similarly to shading with some variations in both cultivars, but seed weight of ‘Misato-zairai’ control was unstable, and was often similar level to S2 (2010 and 2011, Fig. 1). As mentioned above, long sunlight duration around pod and seed formation caused much pod and seed numbers, and shading degree was also associated with these numbers clearly in 2012 (Fig. 1). However, control of ‘Misato-zairai’ could not show the highest pod and seed numbers and 100-seed weight (2011) in the other years, and these were not correlated closely to air temperature and sunlight duration (Fig. 1). Photosynthetic rate does not differ significantly between ‘Fukuyutaka’ and ‘Misato-zairai’ (Hattori et al., 2019), but specific leaf weight and SPAD, the indicators of mesophyll photosynthetic capacity, are often lower in ‘Misato-zairai’ (Nagasuga et al., 2014; Nagasuga et al., 2015). Lower mesophyll photosynthetic capacity would be sensitive to not only air temperature and sunlight duration but also the other environmental factors through the lower utilization of high light intensity for photosynthesis, and these might be associated with unstable seed weight of ‘Misato-zairai’ under the full sunlight condition.

In a previous study (Nagasuga et al., 2019), stratified seed weight was correlated with node number in both cultivars, but the ratio of seed weight to node number increased with the increase in relative light intensity in ‘Fukuyutaka’. In ‘Misato-zairai’, this increase was small at moderate to high relative light intensity. Therefore, we hypothesized that seed weight was decreased by heavy (‘Misato-zairai’) or even light (‘Fukuyutaka’) shading. However the responses of seed weight and yield components in both cultivars to shading were similar in our present study: the effect of light shading on seed weight was not significant in ‘Fukuyutaka’, and seed weight, pod number and seed number were decreased significantly in the order of S1, S2 and S3 in ‘Misato-zairai’ although seed weight of control was unstable. Methodologically, the most critical difference of the current study was the absence of branching vegetation during the reproductive stage, which likely affected the utilization of high-intensity light in seed pro-

**Fig. 5** Correlation between 100-seed weight and seed distribution in ‘Fukuyutaka’ and ‘Misato-zairai’. Data are mean±S.E. (n=10). White, control; light grey, S1; dark grey, S2; black, S3; circles, ‘Misato-zairai’; squares, ‘Fukuyutaka’. **P<0.01;

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