Effects of High Temperature on Flowering and Pod Set in Soybean

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Plants of soybean (cv. Enrei) were grown in pots (1/5000 a) in a vinyl house. Temperature treatment was conducted for 10 days from the beginning of the flowering period (BFP) in the growth chambers under artificial light controlled at day/night air temperatures of 27/27, 32/27, and 37/27°C, respectively. The pollen viability at 37/27°C (89.4%) was significantly lower than 27/27°C (97.2%). In order to identify the sensitive stage to high temperature, the plants were treated for 2 days before BFP in the growth chambers controlled at 27/27 and 40/27°C, respectively, and the pollen viability of flowers opening after the treatment was investigated. By the treatment at 40/27°C, the pollen viability of flowers which opened at 4 days after the treatment (82.9%) was significantly lower than 27/27°C (97.3%). This indicates that floral buds at 4 to 5 days before flowering, which coincide with the microsporogenesis stage, are sensitive to high temperature. However, high temperature affected the pod setting ratio a little in both experiments. High temperature treatment was conducted by transferring the plants into the glasshouse under natural light before and after BFP. High temperature treatment at 7–1 days before BFP promoted vegetative growth and increased the pod setting ratio, while reducing the seed size. High temperature treatment at 14–8 days before BFP promoted floral differentiation on the second order racemes with compound leaves and increased the number of the floral buds, so that reduced the pod setting ratio. These results suggest that high temperature at the microsporogenesis stage reduces pollen viability, however, pod setting ratio is affected by the number of floral buds and nutrient conditions at the flowering stage rather than by the pollen viability.

Key words : Flowering, High temperature, Pod setting ratio, Pollen viability, Soybean

Introduction

Global mean air temperature is predicted to increase by a range of from 1.4 to 5.8°C by 2100[8]. There is considerable concern about the effects of high temperatures on crop production. Many leguminous crops such as cowpea[1,5,17], common bean[3,12,16], and groundnut[2,18,19,20] are sensitive to high temperature, resulting in the reduction in the number of flowers and pod setting ratio. It is well known that abortion of flowers and young pods is an important limiting factor of seed yield in soybean[25] because of the lower pod setting ratio (20 to 60%[28]). Furthermore, temperatures of 33 to 40°C appear to be supraoptimal for growth and development of soybean[9,27]. This study was conducted to clarify 1) effects of air temperature on flowering and pod set, 2) effects of high temperature at the pre-flowering stage on flowering and pod set, 3) effects of high temperature before and after the beginning of the flowering period on yield components of soybean.

Materials and Methods

1. Plant materials

Plants of soybean (*Glycine max* L., cv. Enrei) were grown in a vinyl house to avoid rainfall at the Field Science Center, Faculty of Agriculture, Okayama University (34°41' N, 133°55' E) in 2004 and 2005. The vinyl film transmitted 70% of solar radiation in 2004 and 79% in 2005, respectively. Three seeds each were sown in Wagner pots (1/5000 a) filled with 3.5 kg of sandy loam and 1.2 g of compound fertilizer ($N:P_2O_5:K_2O = 5:15:20$) per pot on June 21, 2004 and June 20, 2005, respectively. After the primary leaves were fully

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expanded, the seedlings were thinned to a single plant per pot. To avoid competition with main stem, all branches were removed as they appeared. The plants were irrigated as required, and normally grown without water stress.

2. *Exp. 1: Flowering and pod set of soybean plants grown under different air temperature conditions (2004)*

At the beginning of the flowering period (34 days after sowing, 34 DAS), four plants each were transferred into the three growth chambers (Tokyo Rikakikai, FLI-301 NH) under artificial light. The growth chambers were controlled at day/night air temperatures of 27/27, 32/27, and 37/27°C, respectively, changing gradually the day/night air temperature over 2-hour periods (Fig. 1). About 350 μmol m^{-2} s^{-1} of photosynthetically active radiation was provided for 12 hours, 07:00 to 19:00 by the fluorescent tubes in the growth chambers. At 10 days after the start of the treatment, the plants were returned to the vinyl house.

At 9 days after the start of the treatment, five floral buds which would open next day were sampled to investigate pollen viability. Anthers were collected from each of the floral buds fixed in ethanol acetate solution (3:1) for 1 hour, and they were split open on a glass slide and stained with 1% water-blue solution. The numbers of viable pollen grains which stained blue and nonviable ones which remained transparent in a 5mm square were counted using a light microscope (Olympus, BX 50). Pollen viability was estimated as the ratio of viable to total pollen grains. Flowers which opened during the treatment for 10 days were marked. Flower or pod shedding of these flowers was monitored and pod setting ratio was calculated. The time course changes in flower opening were examined at 37-39 DAS by using the plants grown in the vinyl house.

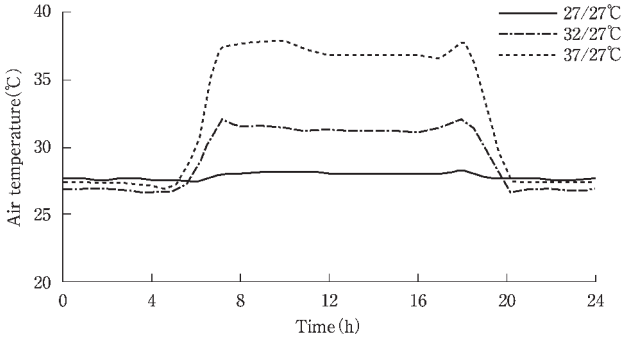

Fig. 1 Mean air temperatures in the growth chambers during the treatment for 10 days (2004).

3. *Exp. 2: Flowering and pod set of soybean plants exposed to high temperature at the pre-flowering stage (2005)*

At the pre-flowering stage (30 DAS), four plants each were transferred into the two growth chambers (Tokyo Rikakikai, FLI-301 NH) under artificial light with the same photoperiod as Exp. 1. The growth chambers were controlled at day/night air temperatures of 27/27 and 40/27°C, respectively. At 2 days after the start of the treatment, the plants were returned to the vinyl house.

At 10:00 every morning, anthers were collected from each of flowers of basal order racemes which opened on that day, and pollen viability was investigated by the same method as Exp. 1. Flower or pod shedding of these flowers was monitored and pod setting ratio was calculated.

4. *Exp. 3: Differences in yield components of soybean plants exposed to high temperature before and after the beginning of the flowering period (2004)*

High temperature treatment was conducted by transferring the plants into the glasshouse under natural light at successive 7-day intervals during 4 weeks before and after the beginning of the flowering period (HT1 to HT4 in turn). The glasshouse was equipped with two ventilation fans; the small one ran from 18:00 to 06:00 to prevent rising air temperature at night, and the other one ran when the air temperature in the glasshouse increased to more than 38°C. The plants grown in the vinyl house during the whole growth period were used as Control. Air temperature at 5-10 cm above the plant canopy in the vinyl house and the glasshouse was measured at 10-minute intervals with Thermo Recorder *Ondotori* (T&D, TR-71S), and the means were stored at successive 1-hour intervals (Table 1).

The dates of flower opening, and of flower or pod shedding were recorded daily for each node position,

Table 1 Mean, maximum, and minimum air temperatures during high temperature treatment (2004)

(°C)		High temperature treatment			
		HT1	HT2	HT3	HT4
Vinyl house (Control)	Mean	32.2	32.4	32.5	31.1
	Max.	40.9	39.9	40.4	38.0
	Min.	23.4	24.9	24.7	24.1
Glasshouse (High temperature)	Mean	33.6	34.0	33.8	33.3
	Max.	43.8	42.6	42.8	42.5
	Min.	23.4	25.4	24.9	24.0

raceme order, and intra-raceme position from the beginning of the flowering period (32 DAS) for three plants of each plot. Raceme order was defined by Torigoe *et al.*[23] as follows. The first order raceme develops from the axil just above the petiole on the stem. The second order raceme develops from right and left axillary buds of the first order raceme, and the third order raceme from those of the second order raceme. The terminal raceme of the stem is called zero order raceme. The zero and first order racemes are defined as basal order racemes, and higher order racemes are collectively called upper order racemes. Some racemes on the upper order racemes have compound leaves. After harvest, the number of nodes, and main stem length and weight were measured for the same plants. Then, yield and yield components were examined.

Results and Discussion

1. Exp. 1: Flowering and pod set of soybean plants grown under different air temperature conditions (2004)

The pollen viability of floral buds just before flowering on the 9th day of the treatment period was significantly ($P < 0.05$) reduced, from 97.2% at 27/27 ℃ to 89.4% at 37/27 ℃, while there was no significant effect of air temperature on the pod setting ratio (Table 2). This result suggested that the decline in the pollen viability by a high day temperature of 37 ℃ during floral bud development had no direct effect on pod set. According to Kato[10], flower and pod shedding of soybean are primarily caused by the undevelopment of embryo and rarely caused by the failure in fertilization. Gross and Kigel[3] also reported that the pod set after fertilization might be reduced by the embryo abortion in common bean. In this experiment, the plants were returned to the normal condition after the investigation of pollen viability. Thus, it seemed that air temperature didn't have much effect on pod setting ratio in this experiment. The total number of flowers per plant which opened during the treatment at 32/27 ℃ for 10 days tended to increase as compared with that at 27/27 ℃ and 37/27 ℃ (Table 2). Although some flowers didn't open, they grew into pods. The number of these flowers was the largest at 27/27 ℃ (data not shown). We found that soybean flowers opened in the morning, especially during 07:00 to 09:00, when air temperature was 28.3 to 32.0 ℃ (Fig. 2). The increase in the number of flowers which opened at 32/27 ℃ was due to air temperature which may be the optimum range for flower opening.

It is known in rice that anther dehiscence occurs by the expansion of pollen, following flower opening[14,15]. In soybean, some flowers grew into pods without opening. Thus, flower opening may not be necessary for fertilization in soybean.

2. Exp. 2: Flowering and pod set of soybean plants exposed to high temperature at the pre-flowering stage (2005)

The pollen viability of flowers which opened at 1 to 5 days after the treatment at 27/27 ℃ for 2 days was constantly high and exceeded 95% (Fig. 3). By the treatment at 40/27 ℃, the pollen viability of flowers which opened within the first 3 days after the treatment for 2 days was not significantly different from 27/27 ℃, but that of flowers which opened at 4 days after the treatment was significantly ($P < 0.01$) reduced to 82.9% (Fig. 3). This number (4 days) indicated that floral buds at 4 to 5 days before flowering were sensitive to a high day temperature of 40 ℃. The pollen viability of flowers which opened at 5 days after the treatment at 40/27 ℃ for 2 days tended to

Table 2 The pollen viability on the 9th day of the treatment period, the total number of flowers per plant opening during the treatment for 10 days, and the ratio of these flowers which grew into pods (2004)

Day/night temperature	Pollen viability[a] (%)	Number of flowers opened per plant[b]	Pod setting ratio[b] (%)
27/27 ℃	97.2 a	15.0 a	65.8 a
32/27 ℃	98.1 a	19.3 a	54.4 a
37/27 ℃	89.4 b	15.3 a	58.6 a

[a] Mean of 5 floral buds.
[b] Mean of 3 plants.
Means followed by the same letter are not significantly different at 5% level according to Fisher's LSD method.

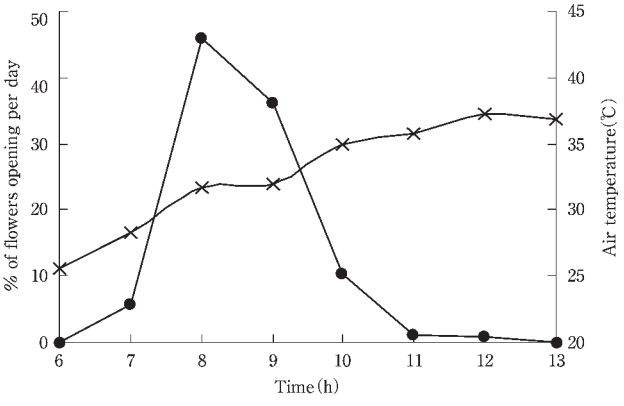

Fig. 2 Time course changes in flower opening (●) and mean air temperature (×) from 37 to 39 days after sowing (2004).

recover to the level at 27/27°C (Fig. 3). 4 or 5 days before flowering tended to coincide with the stage of microsporogenesis[10] or pollen and embryo-sac formation[22], so it was considered that a high day temperature of 40°C caused the inhibition of pollen-mother-cell formation. There was no significant relationship between pollen viability and pod setting ratio (Fig. 4), the same as the result in Exp. 1. This also indicates that flower and pod shedding are rarely caused by the failure in fertilization[10].

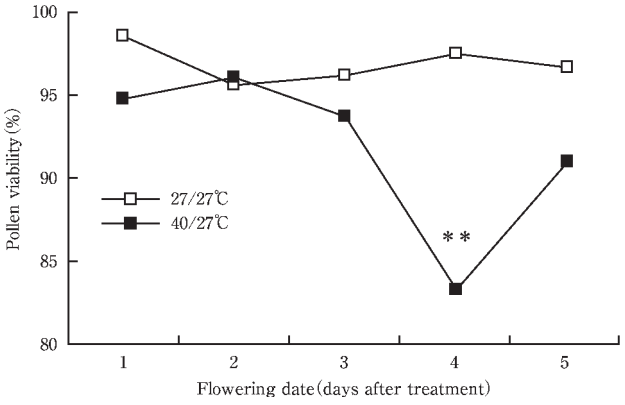

Fig. 3 The pollen viability of flowers which opened after the treatment for 2 days (2005).
**Significant at 1% level.

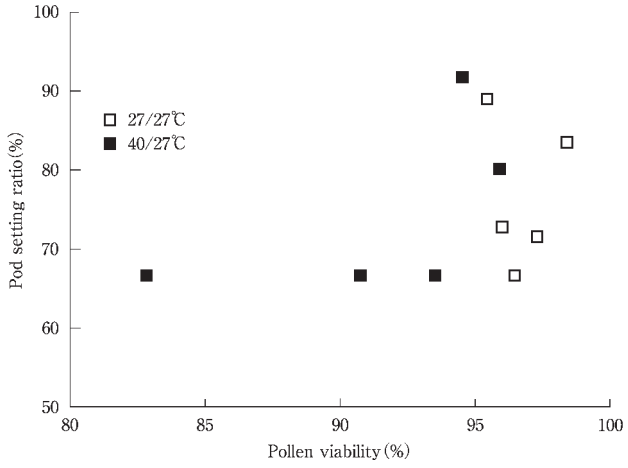

Fig. 4 Relationship between pollen viability and pod setting ratio (2005).

In general, pollen is more sensitive to high temperature than female reproductive structures[16], although effects of high temperature on female fertility cannot be dismissed[3]. It has been reported in cowpea[1,5,17], common bean[3,16], and groundnut[18,19,20] that high temperature during floral bud development, especially microsporogenesis, can reduce pod/seed set due to damage to the pollen mother cells[27], resulting in poor anther dehiscence, and the reduction in pollen number and pollen viability[2,6,13]. Similar effect of high temperature at the microsporogenesis stage on pollen viability was obtained in this experiment, however, the decline in pollen viability by high temperature caused little reduction in pod set. This difference was resulted from the higher level of pollen viability of over 80% even though the plants were exposed to a high day temperature of 40°C. There are several reports that the floral bud temperature of plants grown in growth cabinets is a few degrees cooler than the surrounding air temperature[4,19]. Prasad *et al.*[19] observed in groundnut that there was no difference between air and floral bud temperatures in a growth cabinet at 28°C, but floral bud temperatures were about 1, 2, and 5°C cooler than air temperatures when exposed to 34, 42, and 48°C, respectively. This may be associated with the construction of papilionaceous flower which has three layer petals, a banner petal, two wing petals, and two keel petals. It seemed also in this experiment that floral bud temperature was a few degrees cooler than target air temperature of 40°C, so that pollen viability of over 80% was maintained.

Table 3 Differences in the growth characteristics of soybean plants with high temperature treatment at successive 7-day intervals during 4 weeks before and after the beginning of the flowering period (2004)

	Treatment period (DAS[a])	Number of nodes per plant			Main stem length (cm)	Main stem weight (g)
		Main stem	Racemes with compound leaves	Total		
Control		11.7 a	12.0 a	23.3 b	35.2 a	3.3 c
HT1	21–27	12.0 a	13.3 a	25.3 ab	36.8 a	3.8 bc
HT2	28–34	11.7 a	14.3 a	26.0 ab	36.0 a	3.9 b
HT3	35–41	12.3 a	16.0 a	28.0 a	42.4 a	3.8 bc
HT4	42–48	13.0 a	16.0 a	29.0 a	41.2 a	4.7 a

[a]Days after sowing.
Mean of 3 plants.
Means followed by the same letter are not significantly different at 5% level according to Fisher's LSD method.

3. Exp. 3: Differences in yield components of soybean plants exposed to high temperature before and after the beginning of the flowering period (2004)

Table 3 shows the growth characteristics of the plants exposed to high temperature before and after the beginning of the flowering period. The total number of nodes in high temperature plots (HT1–HT4) was larger than that in Control, due to the increase on the racemes with compound leaves. The plants in these plots had longer and heavier main stem than Control. Uwagoh *et al.*[24] reported similar results with soybean plants grown under high temperature condition in the TGC[7] (Temperature Gradient Chamber) during the whole growth period. The time before and after the beginning of the flowering period was not only the reproductive stage but also the active vegetative stage. It was considered that high temperature promoted vegetative growth.

Table 4 shows the number of floral buds and the pod setting ratio of the plants exposed to high temperature before and after the beginning of the flowering period. There was no significant effect on the number of floral buds. The pod setting ratio in HT1 tended to reduce as compared with that in Control, especially on the upper order racemes. In HT1, the number of flowers opened increased rapidly between 45 and 50 DAS (Fig. 5) because many floral buds were differentiated on the second order racemes with compound

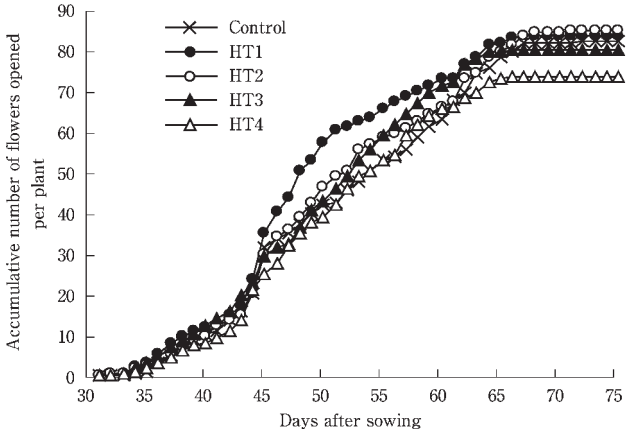

Fig. 5 Changes in the accumulative number of flowers opened (mean of 3 plants; 2004).

Table 4 Differences in the number of floral buds and the pod setting ratio of soybean plants with high temperature treatment at successive 7-day intervals during 4 weeks before and after the beginning of the flowering period (2004)

	Treatment period (DAS[a])	Number of floral buds per plant			Pod setting ratio (%)		
		Basal raceme	Upper raceme	Whole plant	Basal raceme	Upper raceme	Whole plant
Control		15.7 a	85.7 a	101.3 a	27.3 b	29.9 ab	29.1 ab
HT1	21–27	14.7 a	82.3 a	97.0 a	45.2 ab	22.0 b	25.5 b
HT2	28–34	14.7 a	81.0 a	95.7 a	43.2 ab	31.2 a	33.1 a
HT3	35–41	13.3 a	77.7 a	91.0 a	47.4 a	28.7 ab	31.6 ab
HT4	42–48	15.0 a	74.7 a	89.7 a	42.8 ab	25.9 ab	28.6 ab

[a]Days after sowing.
Mean of 3 plants.
Means followed by the same letter are not significantly different at 5% level according to Fisher's LSD method.

Table 5 Differences in the seed yield and the yield components of soybean plants with high temperature treatment at successive 7-day intervals during 4 weeks before and after the beginning of the flowering period (2004)

	Treatment period (DAS[a])	Number of pods per plant	Number of seeds per pod	100 seeds weight (g)	Seed setting ratio (%)	Seed yield per plant (g)
Control		27.3 ab	1.81 a	23.4 a	85.3 ab	9.9 a
HT1	21–27	24.3 b	1.80 a	23.5 a	81.7 b	9.5 a
HT2	28–34	31.7 a	1.85 a	19.2 b	81.3 b	7.9 a
HT3	35–41	28.7 ab	1.80 a	21.0 ab	77.4 b	9.3 a
HT4	42–48	25.7 ab	2.02 a	22.7 a	90.8 a	10.7 a

[a]Days after sowing.
Mean of 3 plants.
Means followed by the same letter are not significantly different at 5% level according to Fisher's LSD method.

leaves. It was considered that too many floral buds on the second order racemes with compound leaves caused by the high temperature from 20 to 27 DAS, which coincided with the floral differentiation stage, led to a decline in the pod setting ratio on the upper order racemes[21]. In HT2, the pod setting ratio was higher than Control (Table 4). Kohri *et al*.[11] observed that nutrient conditions at the pre-flowering stage influenced the floral organ shedding at the post-flowering stage. Thus, it seemed that vegetative growth was promoted by high temperature at one week before the beginning of the flowering period, so that the pod setting ratio in HT2 became higher than Control.

Table 5 shows the seed yield and the yield components of the plants exposed to high temperature before and after the beginning of the flowering period. The number of pods in HT1 was smaller and that in HT2 was larger than Control, which was the same tendency as the pod setting ratio. It is known that the number of pods is primarily determined by the number of floral buds rather than by pod setting ratio[21]. In this experiment, there was small difference in the number of floral buds between plots, so the number of pods was parallel to the pod setting ratio. The seed size (100 seeds weight) in HT2 was significantly ($P < 0.05$) small as compared with that in Control in accordance with the increase in the number of pods[21]. Therefore, the seed yield was not significantly different among the plots.

Conclusion

Higher air temperature (≧37°C) at the microsporogenesis stage reduced the pollen viability, while it affected the pod setting ratio a little. We found that soybean flowers opened in the morning, especially during 07:00 to 09:00. But some flowers grew into pods without opening. Clearly, flower opening is not necessary for fertilization in soybean. Higher air temperature from the pre-flowering stage to the flowering stage (HT2) promoted vegetative growth, so that the pod setting ratio of the whole plant became higher. Instead of an increase in the number of pods, the seed size became smaller. Significant increase in the floral buds on the racemes with compound leaves caused by high air temperature at the floral differentiation stage (HT1) led to a decline in the pod setting ratio. These results suggest that high air temperature at the microsporogenesis stage reduces pollen viability, however, pod setting ratio is affected by the number of floral buds and nutrient conditions at the flowering stage rather than by the pollen viability. In this study, we discussed the effects of higher air temperature on seed yield of soybean through dividing the effects on flowering and pod set. Further studies are needed with higher air temperature than in the present experiment, which should examine more different growth stages and lengths of treatment.

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高温がダイズの開花・結莢におよぼす影響

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ダイズ品種エンレイを供試し，雨除けハウス内でポット栽培を行った．開花始から10日間，昼/夜温を27/27，32/27，37/27℃に設定した人工光型グロスチャンバー内でダイズを育成し，処理９日目に開花前日の花蕾について花粉稔性を調査した．花粉稔性は27/27℃処理（97.2％）に比べて37/27℃処理（89.4％）で有意に低下した．高温に敏感な時期を特定するため，開花始前に２日間，昼/夜温を27/27，40/27℃に設定した人工光型グロスチャンバー内でダイズを育成し，処理後開花した花について花粉稔性を調査した．その結果，処理後４日に開花した花の花粉稔性が27/27℃処理（97.3％）に比べて40/27℃処理（82.9％）で有意に低下した．すなわち開花前４，５日が高温に特に敏感な時期であることが示され，この時期は雄性生殖細胞分裂期に一致した．しかし，両実験とも結莢率におよぼす高温の影響は小さかった．さらに，自然光下のガラス温室内で開花始前後の４週間について１週間ごとに高温処理を行い，収量成立過程におよぼす影響について検討した．開花始前７～１日の高温処理は栄養成長を促進し結莢率を高めたものの，百粒重を減少させたため，子実収量は対照区とほぼ同様となった．開花始前14～８日の高温処理は２次椏枝の花芽分化を促進しその花蕾数を著しく増加させた結果，結莢率が著しく低下した．以上の結果より，雄性生殖細胞分裂期の高温は花粉稔性を低下させるが，結莢率は花粉稔性よりも花蕾数や開花期の栄養条件によって大きく影響されることが示唆された．