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Effects of Soybean Raceme-Order on Pod Set and Seed Growth in Three Cultivars

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Abstract : The characteristics of pod set and seed growth as affected by raceme order were investigated to determine the yield-determining process of soybean. Observations of racemes were made on the 4th, 7th, 10th, 13th and terminal nodes of the main stem of three cultivars (Indeterminate type : Harosoy ; Determinate types : Enrei, Tamahomare). Pod-setting ratio and dry seed weight reduced in higher-order racemes, while the number of seeds in a pod did not vary among raceme orders. The lower seed weight of higher-order racemes was due to the short seed growth period. Compound leaves of secondary racemes enhanced the seed growth but not the pod-setting. With the highest node of determinate types, seed dry weight and rate of dry matter accumulation (RDA) of primary racemes exceeded those of terminal racemes, suggesting that more competition for assimilates among racemes occurred in terminal racemes. The results indicate that, regardless of growth habits, the lower the raceme order, the higher the number of pods and the pod-setting ratio. Seeds derived from lower-order racemes accounted for the majority of the yield. Hence, pod-setting and seed growth of lower-order racemes are more important than those of higher-order racemes in determining soybean yield.
Key words : Dry seed weight, Inflorescence, Pod-setting ratio, Raceme order, Soybean (*Glycine max* (L.) Merr.).

ダイズの花房次位が着莢と子実肥大におよぼす影響 : 磯部勝孝・国分牧衛*・坪木良雄（日本大学農獣医学部・*農業研究センター）

要　旨 : ダイズの収量成立過程を発育形態的な観点から解析するため，有限伸育型品種（エンレイ，タマホマレ）と無限伸育型品種（Harosoy）を用いて花房次位ごとの着莢率と子実肥大の経過を明らかにした．調査は主茎の第4，7，10，13および最上位節について行ない，以下のような結果を得た．いずれの品種とも着莢率と子実乾物重は花房次位が高まるにつれて低下したが，一莢内粒数は花房次位間に一定の傾向は認められなかった．高次の花房で子実乾物重が低下したのは，高次の花房ほど開花が遅くなり，肥大期間が短くなるためと思われた．また，2次花房の複葉は子実の生長を助長したが，着莢には影響をおよぼさなかった．有限伸育型品種の最上位節では0次花房より1次花房のほうが子実乾物重，乾物蓄積率（RDA）とも大きかったが，これは0次花房は1次花房に比べ莢数が多いため同化産物の競合がより著しいためと思われた．以上のように，ダイズでは伸育型の相違にかかわらず，着莢率，子実乾物重のいずれもが低次な花房ほど大きくなることが明らかにされた．したがってダイズの収量は低次な花房に由来する子実の割合が高く，これらの子実の稔実の良否が収量に大きく影響するものと推察される．
キーワード : 花序，花房次位，子実乾物重，ダイズ，着莢率．

The classification of flowers according to developmental morphology is necessary for precise investigation of the yield-determination process of soybean. Flower clusters of soybean were classified into terminal raceme, primary raceme, secondary raceme, tertiary raceme and so on according to the order in the botanical unit series[11]. Flowering occurred from lower- to higher-order racemes and the flowering of each raceme started from the lower nodes up to the higher nodes[11]. The lower the raceme order, the higher the pod-setting ratio[6,7]. Kuroda et al.[7] reported that the increasing yield of soybean at higher densities is associated with the increased share of pods of lower-order racemes. Thus lower-order racemes contributed more to the yield in terms of the number of pods. However, those results[6,7] were obtained only from determinate types of cultivars. In addition, seed weight is one of the important yield components of soybean. In this regard, it is also necessary to clarify the seed growth process in terms of raceme order for precise investigation of the yield-determining process of soybean. In this paper, we characterized the pod-setting ratio and seed growth process with regard to the raceme order in determinate and indeterminate types of cultivars to understand the yield-determining process of soybean.

Materials and Methods

1. Pot Experiment

Pot experiment was carried out in the net room at the National Agriculture Research Center at Tsukuba to clarify the effects of raceme order on flowering, pod-setting ratio and dry seed weight. Five seeds per pot (cultivar : Harosoy, Enrei, Tamahomare) were sown on May 21, 1993 in 1/2000 a pots containing 10 kg of soil (light Andosol), 60 g of compound fertilizer (3-10-10), 20 g of magnesium lime and 45 g of fused phosphate. The seedlings were thinned to a plant in a pot at the expansion stage of the first trifoliate leaf. Investigations were made only on the 4th, 7th, 10th, 13th and top nodes of the main stem (the node with the first trifoliate leaf was numbered as the first node). The number of flowers and the flowering period were observed at each node for each raceme order. After flowering, sepals on each raceme were marked with different colors to determine clearly the raceme order. At maturity, pods and seeds were harvested and classified by each raceme order and then the pod-setting ratio, the number of seeds in a pod and the dry seed weight were measured. Twenty five plants of each cultivar were used for the measurements. Irrigation and insect control was implemented as needed during the cultivation.

2. Field Experiment

The effects of raceme order on the growth process of seeds were classified in field experiment conducted at the experimental field (Andosol) of the National Agriculture Research Center. The same cultivars as in the pot experiment (Harosoy, Enrei and Tamahomare) were used. Two seeds per hill were sown on June 8, 1993 with 70 cm between rows and 20 cm spacing between plants within rows. After emergence, seedlings were thinned to give a single plant per hill at the expansion of the first trifoliate leaf. Before planting the lime magnesium, compound fertilizer (3-10-10%, N-P_2O_5-K_2O) and fused phosphate were applied at a rate of 100 kg/10 a. Each plots consisted of five rows with 11 m long and arranged in a randomized complete block design with two replications. Observations were made only on the 4th, 7th, 10th, 13th and top nodes of the main stem (the node having the first trifoliate leaf was numbered as the first node). The flowering date of each raceme was designated as the date when the maximum number of flowers began to open. The sampling was initiated on Aug. 3 in Harosoy, Aug. 13 in Enrei, Aug. 20 in Tamahomare, respectively, and the subsequent samplings were carried out every fifth day. For each sampling, at least 40 seeds of each raceme order were collected from several plants. Collected seeds were dried at 80°C for 48 hours and the dry seed weight was measured.

Results

1. Pot Experiment

The date and period of flowering for each raceme order are shown in Fig. 1. Flowering initiated from lower to higher order irrespective of cultivar. The flowering of secondary and tertiary racemes initiated from the 4th node of all cultivars, whereas the flowering of primary raceme started on the 4th node in Harosoy, the 7th node in Enrei, the 10th node in Tamahomare. In the highest node of Enrei and Tamahomare, there was no difference in the flowering date between the terminal raceme and the primary raceme. The existence of compound leaves on the secondary raceme did not affect the flowering date and the period in every cultivar.

The pod-setting ratio of each raceme order is shown in Table 1. Except for the 4th node of Tamahomare, the pod-setting ratio of every node became lower as the raceme order became higher. Comparing the pod-setting ratio of terminal raceme with that of primary raceme on the highest node, the ratio of Enrei was higher in the terminal raceme, whereas that of Tamahomare was higher in the primary raceme. The existence of compound leaves increased the ratio of the secondary raceme of Harosoy, but did not increase that of Enrei or Tamahomare.

The number of seeds in a pod and dry seed weight are shown in Tables 2 and 3. In every cultivar the number of seeds in a pod did not vary with raceme order, whereas the dry seed weight increased with lower raceme orders. On the secondary raceme the dry seed weight was increased by the existence of compound leaves. In addition, the heavier dry seed weight was observed more in the primary raceme than in the terminal raceme on the

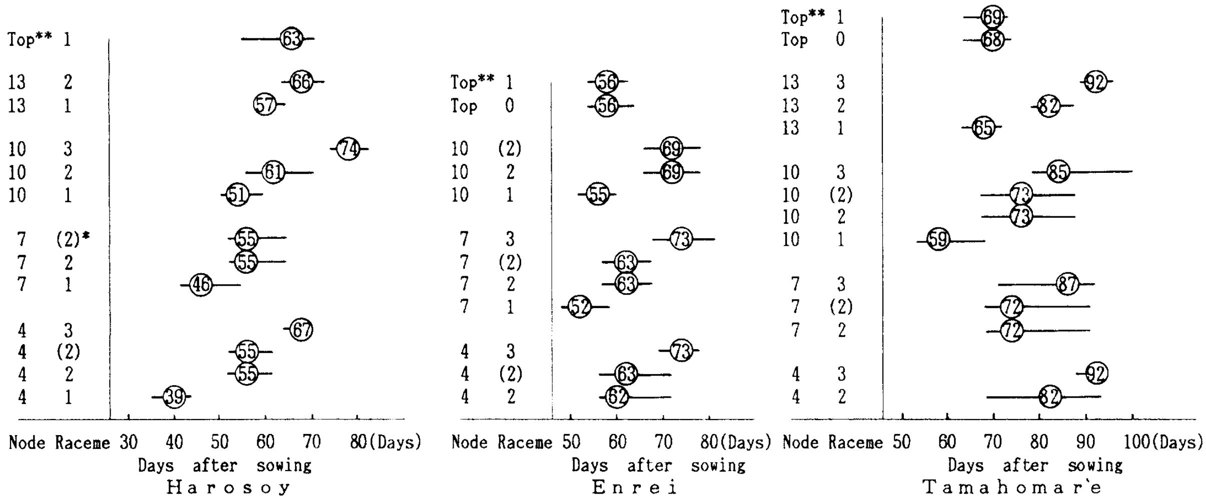

Fig. 1. The flowering period and the flowering date of pot-grown soybeans.
Numbers in circles show the day of flowering and bars show the period of flowering.
* Secondary raceme with compound leaves.
** The node order was 15.0 (Harosoy), 11.4 (Enrei), 15.3 (Tamahomare), respectively.

Table 1. The pod-setting ratio(%) of pot-grown soybeans.

Raceme order	Harosoy					Enrei				Tamahomare				
	Node order					Node order				Node order				
	4	7	10	13	Top+	4	7	10	Top+	4	7	10	13	Top+
3	0.0		0.0			38.1	47.1	35.3		25.0	2.0	16.1	0.0	
(2)++	10.0	40.0				0.0	50.0	70.4			11.6	11.9		
2	7.7	34.8	60.7	6.7		46.8	73.3	73.7		10.7	11.0	19.8	50.0	
1	90.7	61.8	80.0	96.8	77.4		15.9	82.6	50.0			45.2	90.5	76.7
0									58.3					58.3

+The node order was 15.0 (Harosoy), 11.4 (Enrei), 15.3 (Tamahomare), respectively.
++Secondary raceme with compound leaves.

Table 2. The number of seeds in a pod of pot-grown soybeans.

Raceme order	Harosoy					Enrei				Tamahomare				
	Node order					Node order				Node order				
	4	7	10	13	Top+	4	7	10	Top+	4	7	10	13	Top+
3						1.75	1.62	1.78		2.00	2.00	1.60		
(2)++	2.00	2.64					1.50	1.58			0.75	1.20		
2	1.00	2.36	2.43	2.50		1.76	1.82	1.86		1.75	1.47	1.56	2.30	
1	2.59	2.29	1.98	2.53	2.51		1.36	2.21	1.75			1.58	1.74	1.73
0									2.07					1.70

+The node order was 15.0 (Harosoy), 11.4 (Enrei), 15.3 (Tamahomare), respectively.
++Secondary raceme with compound leaves.

terminal node of Enrei and Tamahomare.

2. Field Experiment

Fig. 2 shows the flowering date and period for the different raceme order on each node. The growth of plants in the field experiment was a little poorer compared to that in the pot experiment. The highest node number of the main stem was 13.9 in Harosoy, 11.0 in Enrei and 12.9 in Tamahomare. Flowering occurred from a lower to higher order of racemes in every cultivar.

The dry seed weights of each raceme order and node at maturity are shown in Table 4. The dry seed weights on every node decreased

Table 3. Dry seed weight (mg • seed^{-1}) of pot-grown soybeans.

Raceme order	Harosoy					Enrei				Tamahomare				
	Node order					Node order				Node order				
	4	7	10	13	Top+	4	7	10	Top+	4	7	10	13	Top+
3						288.6	304.1	298.0		120.0	170.0	242.9		
(2)++	230.0	183.5					357.7	358.0			222.0	253.3		
2	210.0	173.0	164.9	158.0		348.3	326.8	347.0		237.5	222.0	268.6	227.5	
1	210.1	231.6	211.0	186.8	165.3		344.4	361.5	407.8			268.6	300.9	308.0
0									355.9					286.1

+The node order was 15.0 (Harosoy), 11.4 (Enrei), 15.3 (Tamahomare), respectively.

++Secondary raceme with compound leaves.

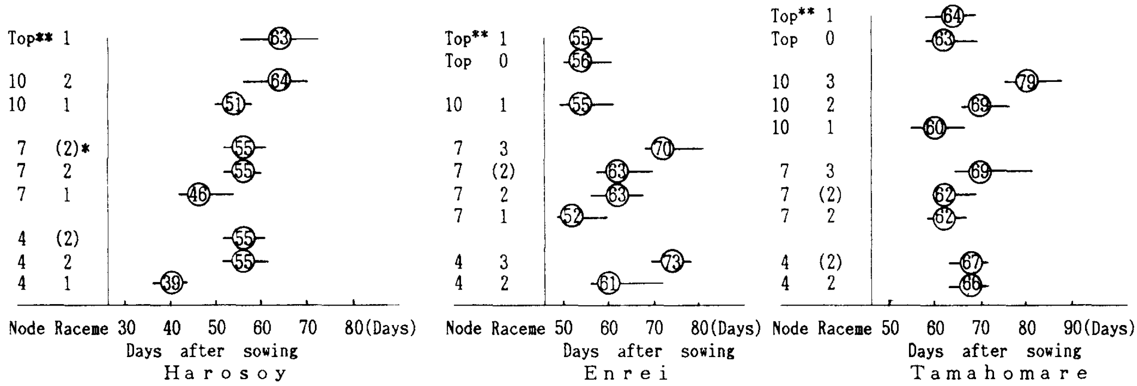

Fig. 2. The flowering period and the flowering date of field-grown soybeans.

Numbers in circles show the day of flowering and bars show the period of flowering.

* Secondary raceme with compound leaves.

** The node order was 13.9 (Harosoy), 11.0 (Enrei), 12.9 (Tamahomare), respectively.

Table 4. Dry seed weight (mg • seed^{-1}) of field-grown soybeans.

Raceme order	Harosoy				Enrei				Tamahomare			
	Node order				Node order				Node order			
	4	7	10	Top+	4	7	10	Top+	4	7	10	Top+
3					257.9	286.4				236.8	252.5	
(2)++	195.0	194.1				315.8			288.3	299.9		
2	190.2	180.8	182.8		279.1	318.8			265.7	285.9	270.9	
1	196.8	235.0	224.0	172.4		325.6	340.6	342.8			300.1	309.4
0								302.4				304.4
	NS	**	*	—	**	**	—	*	*	**	**	NS

+The node order was 13.9 (Harosoy), 11.0 (Enrei), 12.9 (Tamahomare), respectively.

++Secondary raceme with compound leaves.

NS : no significance, * : 5%, ** : 1% level significance, respectively.

as the raceme order became higher regardless of cultivars. Likewise there were significant differences in the weight between the raceme orders except for the 4th node of Harosoy. Comparing the dry seed weight of the primary raceme with that of the terminal raceme on the highest node, it was heavier on the primary raceme in Enrei and Tamahomare, which was statistically significant (5% level) differences in Enrei. In the secondary raceme, except for the 7th node of Enrei, the dry seed weight increased due to the existence of compound leaves.

The rate of dry matter accumulation (RDA) and the effective filling period (EFP) obtained by Daynard's method[2,3] are shown

Table 5. Rate of dry matter accumulation (mg • day^{-1} • $seed^{-1}$) of field-grown soybeans.

Raceme order	Harosoy				Enrei				Tamahomare			
	Node order				Node order				Node order			
	4	7	10	Top⁺	4	7	10	Top⁺	4	7	10	Top⁺
3					8.78	7.72				6.86	6.56	
(2)⁺⁺	5.71	5.92				8.61			7.24	7.26		
2	5.73	5.24	5.66		8.57	8.53			6.60	7.02	7.08	
1	5.64	6.01	5.80	5.11		7.96	8.90	7.76			8.13	8.54
0								7.09				8.41
	NS	**	NS	—	NS	*	—	*	*	NS	*	NS

⁺The node order was 13.9 (Harosoy), 11.0 (Enrei), 12.9 (Tamahomare), respectively.
⁺⁺Secondary raceme with compound leaves.
NS : no significance, * : 5%, ** : 1% level significance, respectively.

Table 6. Effective filling period(days) of field-grown soybeans.

Raceme order	Harosoy				Enrei				Tamahomare			
	Node order				Node order				Node order			
	4	7	10	Top⁺	4	7	10	Top⁺	4	7	10	Top⁺
3					30	37				35	39	
(2)⁺⁺	34	33				37			40	42		
2	34	35	33		32	38			41	41	39	
1	35	39	39	34		41	39	44			37	36
0								43				36
	NS	NS	*	—	*	*	—	NS	NS	*	NS	NS

⁺The node order was 13.9 (Harosoy), 11.0 (Enrei), 12.9 (Tamahomare), respectively.
⁺⁺Secondary raceme with compound leaves.
NS : no significance, * : 5%, level significance.

in Tables 5 and 6. The higher the raceme order, the lower the dry seed weight irrespective of cultivar or node. On the 7th and 10th nodes of Harosoy and the 7th and 10th nodes of Tamahomare, RDA was lower as raceme order increased. On the other hand, EFP became shorter with higher raceme orders, except for the 10th node of Tamahomare. In Enrei and Tamahomare, EFP of the terminal raceme and primary raceme on the highest node was almost the same while RDA was higher on the primary raceme in both varieties. Compound leaves on the secondary raceme did not affect EFP, but RDA of the secondary raceme was increased by the existence of compound leaves, except for the 4th node of Harosoy.

Discussion

The pod-setting ratio of soybean plants was influenced by the flowering date and the podding position (raceme order, node) in the individula plants. The difference in flowering dates between different raceme orders on each node was 10 days on average (Fig. 1). In general, the pod-setting ratio of flowers which opened earlier or emerged on racemes of higher nodes tended to be higher[5,9,10,12,14]. These flowers may have the advantage of receiving more assimilate and the pod set appeared to be determined by the amount of assimilate supplied. In this study, we investigated the pod-setting ratio in terms of raceme order and clarified that the pod-setting ratio increased with lower raceme order regardless of the cultivar. This result agreed with those of Kuroda et al.[6,7]. The flowering started from the racemes of low order up to the racemes of higher order. The pod-setting ratio of Enrei did not significantly decrease in the high-order racemes, probably because the amount of assimilate supplied to each order of raceme might have been almost the same since there was not a large difference in the flowering dates among raceme orders. In comparison with the pod-setting ratios among different nodes of the same raceme order, the ratios of higher nodes were higher than those of lower nodes (Fig. 1, Table 1). This may be because the amount of assimilate distributed was lower in lower nodes than in higher nodes.

In soybean the later the flowering date, the lower the dry seed weight became[4,8,13]. The dry seed weight is determined by the rate of dry matter accumulation of seed and the effective filling period[2,3,13]. Egli et al.[1] reported that in indeterminate types, seed growth rates were relatively constant across the early- and late-flowered pods and the duration of the effective filling period was less in the late-flowered pods. Nagata[8] observed that in indeterminate types, the seeds of later flowering were smaller than those of earlier flowering due to shortened duration of seed growth. Comparing EFP between raceme orders on each node, we recognized that the higher the raceme order was, the shorter the EFP became, except for the 7th node in Harosoy and the 10th node in Tamahomare (Tables 4, 6). Thus lower dry seed weight of high-order racemes was caused by the shorter EFP.

Yoshida et al.[14] investigated the effects of the period of flowering on the number of seeds in a pod and found that the later the pod emerged, the number of seeds in a pod decreased. Judging from this finding , we expected that the number of seeds in a pod which originated from the primary raceme would be more than that of racemes of other orders. Our results did not agree with this expectation. However, the significant correlation between the pod-setting ratio and the number of seeds in a pod was observed in Enrei ($r=0.624^*$). There is therefore a possibility that the number of seeds in a pod emerged from higher nodes, or from the primary raceme, would be more. We could not verify the possibility from our results. At any rate, it appears that the number of seeds in a pod was not influenced by raceme orders as much as the pod-setting ratios.

With the secondary raceme, the existence of compound leaves did not always raise the pod-setting ratio (Table 1). However the dry seed weight and RDA of secondary racemes were increased by the existence of compound leaves, except for the 7th node of Enrei. In other words, compound leaves of secondary racemes affected the seed growth but did not affect the podding. Compound leaves of secondary racemes develop from the period of flowering to early seed growth of the racemes, and expand fully during the seed growth period of the racemes. The translocation of assimilate from compound leaves to the racemes appeared to occur after seed growth was initiated. Contrary to our result, Kuroda et al.[6] reported that the pod-setting ratio of secondary and tertiary racemes became higher due to the existence of compound leaves. Whether the existence of compound leaves might contribute to the pod-setting or not needs further study.

When the dry seed weight and RDA of terminal racemes was compared with that of primary racemes in Enrei and Tamahomare, dry seed weight was heavier and RDA was higher in the primary raceme. This may be because the competition for assimilate was more severe in terminal racemes than in primary racemes since there are a greater number of pods in terminal racemes than in primary racemes (Tables 4—6).

In conclusion, the lower the raceme order, the higher the pod-setting ratio and dry seed weight. With the same raceme order, the pod-setting ratio and the dry seed weight became higher on higher nodes regardless of varieties. This difference caused by raceme order appeared to reflect the amount of assimilate distributed to each raceme. Kuroda et al.[7] reported that in determinate types of cultivars, pods of lower order racemes were more contributory to yield. In this study, we observed the same phenomenon in the indeterminate type of cultivar as well. In addition, the racemes of lower orders showed heavier weight per seed. Thus lower-order racemes accounted for a majority of seed yield regardless of growth habit. In other words, soybean yield would be affected more by pod set and seed growth of lower-order racemes than those of higher-order racemes. Therefore, it is critical for the improvement of soybean yield that the flowering and subsequent seed growth of lower-order racemes occur under a favourable environment.

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