Flowering Control in Orchardgrass (*Dactylis glomerata* L.)

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In relation to the differentiation and development of inflorescence, three developmental stages, *i.e.*, juvenile, inductive and post-inductive stages, are recognized in a few temperate forage grasses including orchardgrass.[1,2,4,21] The juvenile stage* lasts for several weeks after germination in these grass species.[1,2,4,19] Seedlings during this stage are not responsive to any conditions which later promote flowering.[4] After the juvenile stage, plants require short day-length and low temperature for floral-induction.[1,7,8,21,23] Floral-induction has been defined as formation of flowering hormone or chemical changes in plant[7] and thus the post-induction, which means inflorescence differentiation and development, occurs under the subsequent long day-length at moderate temperature after the floral-induction has been attained.[1,4,7,8,21,23] In orchardgrass, however, inconsistent results have been reported about the duration of juvenile stage and the effective range of day-length and temperature for floral-induction.[2,3,4,7,8,19,20,23,25] Therefore the author et al. carried out a series of experiments to clarify influence of major environmental factors and plant-age on floral-induction in orchardgrass. The results obtained are summarized in this paper.

Experimental method

The method of experiments is shown in Fig. 1. Seedlings were grown for several weeks after sowing under continuous light at moderately high temperature (25°C day/15°C night). Seedling-age was expressed by the number of weeks after sowing. In addition, aged tillers were prepared by separating clonal plants which were grown under the growth condition mentioned above for longer than 6 months. In general, floral-induction of orchardgrass is completely inhibited under continuous light at moderately high temperature.[4,7,8,20,23,25] Floral-induction treatments of different day-lengths and temperatures were continued for the minimum of 4 days to the maximum of 54 days. Thereafter, their heading behavior was observed under continuous light at moderately high temperature for 5 to 6 weeks in order to estimate the degree of floral-induction attained by the preceding treatments with a few exception, in which a short period of low temperature (10°C) under continuous light was interpolated just after floral-induction treatments.

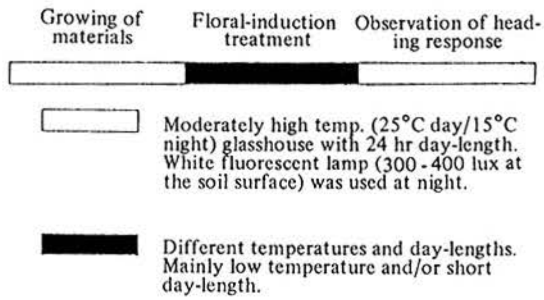

Fig. 1. Experimental method for studying response of orchardgrass to floral-induction treatment

*: The juvenile stage is referred to as the basic vegetative growth stage in other species such as rice plant (*Oryza sativa* L.).[24]

Table 1. Response of 7-week-old seedlings to floral-induction treatment of 8 hr day-length in different periods

Cultivar	Period of treatment[a]	Mean temperature (°C)	% of plants with[b]	
			Heading	Primordia
Aonami	A	7.9	45	80
	B	10.5	78	95
	C	10.7	80	95
	D	14.8	25	50
Latar	A	7.9	26	58
	B	10.5	68	93
	C	10.7	55	100
	D	14.8	0	30
Ab. S 143	A	7.9	5	55
	B	10.5	10	65
	C	10.7	20	80
	D	14.8	0	10

a) A: Oct. 25 to Dec. 6, 1974 B: Mar. 26 to May 7, 1974
C: Oct. 11 to Nov. 22, 1974 D: Apr. 23 to June 4, 1974

b) Percentages of plants with heading inflorescence and inflorescence including primordium, respectively

Optimum temperature and day-length for floral-induction in seedlings[9,10]

Short day-length and low temperature have been regarded as the two major factors which cause floral-induction in orchardgrass.[2,3,4,7,8,19,20,23,25] Gardner and Loomis[7] showed that both short day-length shorter than 12.5 hr and low temperature of 5 to 10°C were obligatorily required for successful floral-induction. Other workers,[8,23] however, reported that only short day-length was essential in floral-induction though short-day induction was more effective at low temperature than at high temperature. On the other hand, Calder[4] suggested that floral-induction depended on a number of cycles of light and darkness with a minimum period of 7 hr darkness each day, because floral-induction occurred under 17 hr day-length. Our results indicated that the maximum response of 7-week-old seedlings to floral-induction treatments of 8 hr day-length was obtained in two periods, one in spring and the other in autumn, during which the mean temperature was about 10°C in all the three materials, "Aonami," "Latar" and "Ab. S143" (Table 1). It was also found out that, under the natural low temperature of about 10°C, floral-induction of the 7-week-old seedlings occurred most effectively in the range of day-length of 9 to 11 hr in "Aonami," 8 to 13 hr in "Latar" and 11 to 12 hr in "Ab. S143," and that shorter or longer day-length than those ranges mentioned above was less effective for floral-induction in each material. From these and earlier workers' findings, it is inferred that floral-induction in seedlings occurs most effectively under the combination of low temperature of about 10°C and short day-length of 10 to 12 hr and that there are differences among materials in the optimum temperature and day-length for floral-induction.

Influence of fertility-level and planting density on the responsiveness to inductive conditions[11,12]

Fertilizer (mainly nitrogen) application and low planting density sometimes promote the differentiation and development of inflores-

Table 2. Response of aged tillers grown at different fertility-levels to floral-induction treatment of 10°C and 12 hr day-length a)

Clone	Fertility-level b)	Period of floral-induction treatment (day)					
		0	4	7	10	14	21
A-101	None			V, V	V, V	V, V	V, V
	Low			V, V	V, V	V, R	27, 19
	Medium			V, V	V, V	V, 25	17, 17
	High	V, V		V, V	V, V	R, 29	17, 16
L-102	None			V, V	V, V	V, R	R, 42
	Low			V, V	R, 26	38, 26	22, 21
	Medium			R, R	R, 30	36, 26	28, 21
	High	V, V		R, 35	32, 24	33, 25	23, 20
E V72-2	None			V, V	V, V	R, R	R, 22
	Low			V, V	V, R	V, R	16, 14
	Medium			V, V	R, 25	15, 15	15, 14
	High	V, V		R, 14	18, 17	15, 14	8, 8
J-100	None		V, V	V, V	V, V	R, R	
	Low		V, V	V, R	29, 22	17, 17	
	Medium		R, R	23, 22	21, 20	21, 17	
	High	V, V	R, R	R, 36	23, 23	17, 17	

a) Two tillers were treated for respective treatment periods, and the results are shown individually.
Figures: The number of days from the end of treatment to heading.
R: Inflorescence primordium was formed on an apex of the main stem.
V: An apex of the main stem remained at vegetative stage.
b) For the none, low, medium and high fertility-level, 14-14-14 fertilizer was applied at the rate of 0, 3, 6 and 12 g/Wagner pot (1/5,000 *are*), respectively. Four tillers were planted per pot and grown for 30 days at each fertility-level. Before the floral-induction treatment, the tillers to be used were transplanted to pots of the medium fertility-level.

Table 3. Heading response as influenced by the seedling-age at the beginning of floral-induction treatment

Material	Treatment		% of plants with a)		No. of leaves on main stem b)		Plant height c) (cm)	
	Seedling-age (week)	Period of treatment (week)	Heading	Primordia	X_1	X_2	Y_1	Y_2
Aonami	4	6	36	79	4.0	11.2	15.0	12.1
	5	5	57	100	5.4	11.1	18.8	16.4
	6	4	57	79	6.9	11.2	22.4	22.7
	7	3	14	42	7.9	10.5	30.7	31.9
Nakei EV-No. 1	4	6	93	93	4.0	11.3	16.3	12.9
	5	5	86	100	5.6	11.4	21.5	17.9
	6	4	86	93	7.0	11.1	26.4	28.1
	7	3	64	93	8.1	10.6	33.1	34.0

a) Refer to foot-note b) of Table 1.
b) Number of leaves emerged on main stem at the beginning (X_1) and at the end (X_2) of the treatment
c) Plant height at the beginning (Y_1) and at the end (Y_2) of the treatment

cence in orchardgrass.[5,23,26] But, the effects of these factors on floral-induction have not been well-known. In the first experiment to clarify this point, aged tillers grown at different fertility-levels were subjected to floral-induction treatment of 10°C and 12 hr day-length for 0, 4, 7, 10, 14 and 21 days. The number of days required for floral-induction differed from clone to clone, but, became smaller as the fertility-level became higher in all the four clones tested (Table 2). In addition, it was shown that the trimming of upper expanded leaf blades had only a little effect on the responsiveness of the tillers grown at high fertility-level to floral-induction treatment. In the second experiment, 7-week-old seedlings of "Aonami" and "Latar" grown at four planting densities and two fertility-levels were subjected to floral-induction treatment of natural low temperature and short day-length for 6 weeks in autumn, 1976. The results indicated that the responsiveness to floral-induction treatment substantially increased when seedlings were grown at low planting density and high fertility-level. From the above results, it is concluded that the responsiveness to inductive conditions in orchardgrass increases when plants grow well-nourished.

Relationship between plant-age and the responsiveness to inductive conditions

1) Duration of juvenile stage[12]

To determine the duration of juvenile stage, seedlings of "Aonami" and "Nakei EV-No. 1" were subjected to the floral-induction treatment of natural low temperature and short day-length in autumn, 1977, for the period from 4, 5, 6 or 7 weeks old to 10 weeks old, respectively. The results showed that the 5-week-old seedlings were responsive to floral-induction treatment in both materials, because the treatment started with 5-week-old seedlings was the most effective (Table 3). Calder[4] reported that juvenile stage lasted for about 5 weeks after germination. But Kozumplik and Christie[19] insisted that juvenile stage was completed when the 8th leaf emerged on the main stem. In our experiment, it took about a week after sowing to germinate and 5th or 6th leaves were emerging about 4 weeks after germination. Therefore, the duration of juvenile stage was somewhat shorter in our experiment than in the earlier workers'.[4,19] In "Aonami", however, the treatment started with 4-week-old seedlings was less effective than that started with 5-week-old seedlings, although the seedling-age and the plant stage expressed by leaf number of main stem increased in parallel until the end of the treatments. When the treatments were started at younger seedling-age, the plant height of seedlings remained lower until the end of the treatments. From this close relation of plant height to seedling-age at the beginning of treatments, it was suggested that the responsiveness of seedlings to inductive conditions was influenced not only by the seedling-age and the plant stage expressed by leaf number but also by the size of the seedlings. Concerning this point, Broué[2] reported that the duration of juvenile stage was shortened under long day-length. As mentioned previously, good nutritive conditions of seedlings may cause high responsiveness to inductive conditions.

In another experiment, 3, 4, 5, 6 and 7-week-old seedlings of "Aonami," "Latar," "Ab. S143," "O.S.G.-7," "Nakei EV-No. 1" and "*Dactylis glomerata* ssp. *judaica*" were subjected to floral-induction treatment of natural low temperature and short day-length for 6 weeks in spring, 1977. In all the materials tested, the effects of the treatment increased linearly with the seedling-age up to 6 weeks, but the effects on the 7-week-old seedlings were almost the same or a little higher than those on the 6-week-old seedlings. From these results, it was concluded that the 6-week-old seedlings grown under continuous light at moderately high temperature were considerably responsive to inductive conditions irrespective of materials.

Table 4. Influence of plant-age on the responsiveness to floral-induction treatment of short day-length and low temperature in "Aonami"[a)]

Plant-age	Period of floral-induction treatment (week)			
	2	3	4	5
7-week-old seedling	0% (29%)	14% (43%)	21% (93%)	71% (100%)
Aged tiller	53 (97)	93 (100)	100 (100)	100 (100)

a) Figures and those in parentheses show the percentages of plants with heading inflorescence and with inflorescence including primordium, respectively.

Table 5. Influence of seasonal change in temperature and day-length on floral-induction in aged plants

Period of treatment[a)]	Mean temperature (°C)	Day-length (range: Min.-Max.)	Percentages of clones[b)]			
			Aonami	Latar	Ab. S143	EV-700
Feb.	5.3	10:22–11:37	100 100	100 100	83 100	100 100
Apr.	15.8	12:35–13:51	100 100	100 100	67 100	100 100
June	19.0	14:32–14:43	83 83	83 100	50 83	100 100
Aug.	22.9	12:54–14:04	0 67	17 33	0 17	100 100
Oct.	17.0	10:23–11:50	100 100	67 100	33 67	100 100
Dec.	6.0	9:37– 9:51	83 100	83 100	67 83	100 100

a) Aged tillers were subjected to floral-induction treatment of outdoor- or unheated glasshouse-temperature with natural day-lengths for 5 weeks from the 1st date of each month.

b) Upper and lower figures show the percentages of clones with heading inflorescence and with inflorescence including primordium, respectively.

2) Increase of the responsiveness to inductive conditions with plant-age[13,14]

To know influences of plant-age after juvenile stage on the responsiveness to inductive conditions, the responsiveness of 7-week-old seedlings was compared with that of aged tillers. First, it was found out that the period required for floral-induction was conspicuously shorter in the aged tillers than the seedlings when both of them were exposed to natural low temperature and short day-length in autumn, 1977 (Table 4). Second, it was clarified that floral-induction was almost entirely prevented by continuous light independently of temperature conditions in the seedlings but was brought about only by low temperature of about 10°C even under continuous light in the aged tillers.

On the other hand, influences of seasonal change in temperature and day-length at Nishinasuno (N 36°55′) on floral-induction of the aged tillers were investigated. The results are shown in Table 5. Floral-induction was effectively promoted in the mean temperature from 5.3 to 15.8°C in "Ab. S143" and 5.3 to 19.0°C in "Aonami" and "Latar." The whole range of mean temperature used in these experiments (5.3 to 22.9°C) was effective on floral-induction in "EV-700." Day-length changed seasonally from the minimum of 9 hr 37 min to the maximum of 14 hr 43 min. This range of day-length was shorter than the critical day-length for floral-induction of the aged tillers in all the materials tested.

From the above results, it may be concluded that the responsiveness of orchardgrass to inductive conditions increases with the plant-age and that the effective range of temperature and day-length for floral-induction is markedly wider in aged plants than in seedlings just after juvenile stage.

Heading behaviour of lateral tiller buds as influenced by floral-induction of main stem[18]

It has been considered that the dependence of lateral tillers on the main stem in heading behavior is lower in perennial grass species than in annual grass species.[6,22] Gardner and Loomis[7] observed in orchardgrass that, when plants were injured by severe freezing after floral-induction, all the newly emerged lateral tillers remained at vegetative stage, and suggested that induction stimulus was localized in the apical growing points which were injured. If this suggestion is true, individual tillers within a plant have to respond independently of each other to inductive conditions. In this case, it may be questioned whether or not the juvenile stage is recognized in lateral tiller buds. To solve this question, heading behavior of lateral tiller buds, which were still kept in the leaf sheaths of aged tillers (main stem) during floral-induction treatment, was investigated. When the period of treatment was not long enough to cause the heading of main stem, none of the lateral tillers reached heading. As the period of treatment became longer, the number of lateral tillers which reached heading became larger in all the three clones tested, though the tendency in the increase of the number of lateral tillers which reached heading was markedly different from clone to clone (Table 6). In addition, after the treatment was carried out for 21 days, only a part of the primary tillers reached heading and all the secondary tillers remained at vegetative stage in both clones of A-101 and L-102. In EV72-7, however, all the primary tillers and about half of the secondary tillers reached heading and some of the tertiary tillers formed inflorescence primordia on their apicies. From these results, it is presumed that induction stimulus of main stem can be transmitted to the apicies of lateral tiller buds to varying extents according to materials.

Table 6. Total number of lateral tillers which reached heading after floral-induction treatment given to main stem[a),b)]

Clone	Period of floral-induction treatment (day)			
	7	10	14	21
A-101	—, —	—, —	—, 0	2, 3
L-102	—, 0	0, 0	0, 1	1, 2
EV72-7	—, 2	4, 6	6, 7	9, 13

a) Materials were the same plants that were grown at high fertility-level in Table 2.
b) Bars show that main stem did not reach heading. Data of two plants used for each treatmental plot are shown individually.

Interaction of day-length and temperature for floral-induction and inflorescence differentiation[15,16,17]

Wilson and Thomas,[25] and the author et al.[15] found out that high temperature under short day-length conspicuously reversed the later phases of floral-induction but somewhat promoted the initial phases of it. On the other hand, Gardner and Loomis[7] recognized that floral-induction was brought about when short day-length at high temperature preceded low temperature under long day-length. Broué and Nicholls[3] also reported that inflorescence

Table 7. Relationship between the effect of low temperature treatment (10°C, 24 hr day-length) on heading response and the degree of floral-induction attained by the preceding short-day treatment (10 or 20°C, 10 hr day-length) in a clone of *Dactylis glomerata* ssp. *judaica*[a)]

Short-day treatment		Low temperature treatment			
Days	Temp. (°C)	0 day	1 day	4 days	7 days
4	10	V_2	V_2	R_2	27.5
21	20	21.0	20.5	21.5	21.0
21	10	16.5	18.0	19.0	21.0

a) Two tillers were tested at respective treatment-combinations.
Figures: Mean number of days from the end of short-day treatment to heading.
V_2: Both tillers remained at vegetative stage.
R_2: Inflorescence primordium was formed on an apex of main stem in each of tillers tested.

Table 8. Influence of low temperature just after floral-induction treatment on heading response

Material	Period of induction treatment	Temperature regime	% of plants with[a)]		No. of heading tillers per 20 plants	No. of days to heading[b)]
			Heading	Primordia		
Nakei EV-No. 1	26 days	Control	75	100	48	19.5
		Low temp.	90	100	74	23.8
	40	Control	100	100	105	18.8
		Low temp.	100	100	130	22.8
Aonami	33	Control	35	95	11	24.6
		Low temp.	70	100	38	25.6
	54	Control	95	100	96	21.9
		Low temp.	100	100	125	23.7
Latar	33	Control	55	85	31	24.5
		Low temp.	80	95	43	29.3
	54	Control	95	100	81	25.7
		Low temp.	95	100	104	29.1

a) Refer to foot-note b) of Table 1.
b) Mean number of days from the end of floral-induction treatment to heading of main stem

differentiation just after floral-induction was pronouncedly promoted by low temperature under long day-length. The results of our experiments using a clone of "*Dactylis glomerata* ssp. *judaica*" were almost agreeable to the above findings and suggested that low temperature response played relatively more important roles after short-day response in floral-induction and inflorescence differentiation than before short-day response. In this clone, however, it was shown that the promotive effects of low temperature after short day-length were closely related to the degree of floral-induction attained under the preceding short day-length, that is, low temperature after short day-length promoted the heading of partially induced tillers but retarded the heading of completely induced tillers (Table 7).

Accordingly, influences of low temperature just after floral-induction treatment on heading behavior were investigated for cultivars of orchardgrass. The 6-week-old seedlings of "Aonami," "Latar" and "Nakei EV-No. 1" were subjected to floral-induction treatment of 9 hr day-length under natural low temperatures in autumn, 1978, for two different periods. After the treatments, their heading behavior was observed under continuous light with two temperature regimes: 1) Control regime, 35 days of high temperature (25°C day/15°C night); 2) Low temperature regime, 7 days of low temperature (10°C const.) followed by 28 days of high temperature. For all the materials, the percentages of plants with heading tiller were markedly higher under low temperature regime than under control regime after the short period of treatment. Almost all the plants, however, reached heading regardless of temperature regimes after the long period of treatment. Heading tillers increased as the period of treatment became longer, and still more increased under low temperature regime (Table 8). Heading began a few days later under low temperature regime than under control regime. But under low temperature regime, heading tillers increased promptly in number after the onset of heading and the period of heading was apparently shortened. From the above results, it is considered that low temperature given just after the completion of floral-induction treatment is able to decrease the percentage of non-heading plants, to increase the number of heading tillers and to synchronize their flowering through the effects on inflorescence differentiation.

On the basis of the overall knowledge presented in this paper, a method of accelerating the cycle of generations for breeding purpose in orchardgrass has been established.

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