Influence of Ageing on Photo- and Thermo-Control of Seed Germination in Grand Rapids Lettuce (*Lactuca sativa* L.)

Yoshihiro SUZUKI

Faculty of Education, Fukushima University, Matsukawa-Machi, Fukushima, 960-12 Japan

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The reversible photoreaction of R (Red light) and FR (Far-red light) controlling the seed germination in Grand Rapids lettuce (*Lactuca sativa* L.) varies markedly not only with germination temperature, but also with the physiological state of seed caused by ageing. The photoreversibility in Grand Rapids lettuce seeds is more evident in the dormant (fresh) and deteriorating (60 and 66 months after harvest) seeds. The reversibility in the non-dormant seeds, however, can be induced again by a prolonged exposure to FR light or high (40°C) temperature pretreatment after the onset of imbibition. The velocity and the viability in germination of the seeds exposed to the prolonged FR light or heat-sensitized at 40°C for 48 hr maintained for a longer time than in the seeds having no exposure to FR light or heat-sensitization. The photoreversible induction by the prolonged exposure to FR light is due to the secondary photo-dormant stage of the seeds. The photo-reversible induction by a heat-sensitization after the onset of imbibition, on the other hand, is due to the two different physiological states of the seed; a, the secondary thermo-dormant stage caused at 40°C for 48 hr, and b, the deteriorating stage caused by the thermal injury at 40°C for 144 hr. Germination induction effects in the heat-sensitized seeds with high temperature pretreatment after the onset of imbibition are greater in GA₃ than in R light.

INTRODUCTION

The germination of light-sensitive seeds is controlled by a reversible photoreaction.¹⁻⁵⁾ There is, however, considerable variation between different seed stocks, which depends largely on the history of the parent plant,^{6,7)} and the seeds after harvest.⁸⁻¹⁰⁾ There are only a few precise data on the relationships between the physiological states of seeds caused by ageing and germination temperature under the phytochrome control of seed germination.

The present paper reports the photo- and thermo-control system in lettuce seed germination at various temperatures, using the seeds in different physiological states, that is, dormant, non-dormant and aged ones.

MATERIALS AND METHODS

Lettuce plants (*Lactuca sativa* L. Grand Rapids) were grown in the green house of Fukushima University in 1978. Seeds were harvested from the mother plants about 23 days after anthesis. Harvested seeds were air-dried (5.9–6.8% water contents in seeds) and kept in paper bags in a wooden box at a controlled temperature (20±2°C) until used.

Fifty seeds were sown on two layers of Tōyō No. 3 filter paper moistened with 1 ml distilled water in a 4-cm diameter Petri dish. The dishes were then wrapped in a light-proof paper, which was removed when irradiation was given, 8 hr after the beginning of the dark period.

Heat-sensitization and prolonged FR light irradiation were carried out as follows: fifty non-dormant (24 months after harvest) seeds were exposed to 20°C for 4 hr dark period after they were sown on two layers of Tōyō No. 3 filter paper moistened with 1 ml distilled water in a 4-cm diameter Petri dish, and then were wrapped with a light proof paper. They were exposed to 40°C in a moist chamber for various hours, or exposed to FR light at 20°C for 48 and 144 hr. The light-proof paper was removed from the dish at the time irradiation was given, the solution was changed from distilled water to GA₃ 10⁻³ M solution, or GA₃ 10⁻³ M solution to distilled water, and 0.2–0.4 ml distilled water was added at 48 hr interval to prevent drying in Petri dish.

R (660 nm) and FR (730 nm) lights were obtained by biological spectrograph,^{9,10)} and light intensity at the level of seed was adjusted to 3.0 Wm⁻² for R and FR lights.

The percent germination was determined 48 hr after sowing or the transferring of the seeds at 20 or 25°C after prolonged exposure to FR light or heat-sensitization, and is expressed as an average of four dishes with a $\pm$ standard error.

RESULTS

Variability of photoreversible induction by R and FR lights in germination

Grand Rapids lettuce seed showed phytochrome control of germination both at 15 and 20°C when they were sown immediately after seed harvest (Table 1). They, however, did not show any reversibility both at 15 and 20°C with 6, 12 and 24 months after it, because they germinated more than 94% in darkness or under 5-min FR light irradiation. They showed completely reversible at 25°C with 0 month after harvest. The reversibility, however, began to decrease with 6, 12 and 24 months, and increased again with 36, 48, 60 and 66 months. At 30°C, they showed completely reversibility with 6, 12, 24 and 36 months after harvest, but their germination rate did not show more than 84% even by 5-min exposure to R light (Table 1). Their reversibility, however, did not show at 30°C with 0, 60 and 66 months after harvest, because they did not germinate by 5-min exposure to R light at 30°C.

The 24-month-aged seeds which had become non-photoreversible by 5-min exposure to R and FR lights at 20°C can induce again their reversibility by prolonged (48 or 144 hr) exposure to FR light (Fig. 1). Their reversibility, also can be induced again at the germination temperature of 20°C by heat-sensitization at 40°C for 24, 48, 72, 96 and 120 hr after the onset of imbibition (Table 2).

Effects of R light or GA₃ on germination in the seeds exposed to the prolonged FR light or heat-sensitized

The seeds irradiated at 20°C for 48 or 144 hr with 24, 36 and 48 months after harvest germinated 91–98% respectively at the germination temperature of 20°C by the application of GA₃ (Fig. 2).

The heat-sensitized seeds kept at 40°C for 48 hr with 24 months after harvest germinated 61–62% at the germination temperature of 20°C in darkness or by 5-min

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* GA₃: Gibberellic acid A₃ are purchased from Wakō Chemicals Co., Japan.

Table 1 Germination of lettuce seeds after exposure to R* (5-min) and FR** (5-min) radiation in sequence.

Germination temperature (°C)	Irradiation***	Germination following seed storage for indicated months (%)							
		0	6	12	24	36	48	60	66
15	Dark	82±2	100	98±1	99	98±1	89±1	47±3	33±2
	R	99±1	100	100	100	98±1	99±1	98±1	99
	FR	57±3	96±2	95±2	97±2	81±3	58±3	27±2	22±1
	F-FR	66±2	99	98±1	98±1	84±3	61±3	36±2	35±1
	F-FR-R	97±3	98±1	99	100	98±2	97±1	99	97±1
20	Dark	47±3	99	100	99	100	92±2	25±3	19±2
	R	96±2	99	100	100	99	98±1	97±2	99
	FR	7±1	94±4	97±1	98±2	67±2	49±3	18±1	15±3
	R-FR	24±2	100	99	97±1	78±3	62±2	39±3	26±2
	R-FR-R	95±2	98±1	100	99	100	100	99	97±1
25	Dark	6±1	80±3	93±2	88±2	73±2	51±3	0	0
	R	88±3	100	99	99	100	97	93±2	99
	FR	1	59±2	78±3	69±3	25±1	18±2	1	1
	R-FR	8±1	63±2	83±2	74±3	36±3	25±3	5±1	6±1
	R-FR-R	93±3	99	100	98±2	97±2	98±1	92±1	97±2
30	Dark	0	0	0	0	0	0	0	0
	R	0	71±3	76±3	65±2	47±4	18±1	0	0
	FR	0	0	0	0	0	0	0	0
	R-FR	0	0	0	0	0	0	0	0
	R-FR-R	0	79±1	84±2	78±3	58±2	27±2	0	0

* R: Red light.

** FR: Far-red light.

*** Irradiation was given 8 hr after the beginning of dark period.

Fig. 1 Germination of the prolonged FR light-irradiated seeds after exposure to R (5-min) and FR (5-min) radiation in sequence.

A, FR light-irradiation for 48 hr; B, FR light-irradiation for 144 hr.

Table 2 Germination of heat (40°C)-sensitive lettuce seeds after exposure to R (5-min) and FR (5-min) radiation.

Germination temperature (°C)	Irradiation**	Germination (%)						
		Heat-sensitization* (hr)						
		24	48	72	96	120	144	168
20	Dark	15±1	0	0	0	0	0	0
	R	94±2	91±2	92±2	93±2	33±2	8±1	1
	FR	71±1	9±1	7±1	0	0	0	0
	R-FR	80±3	14±2	14±1	6±1	5±1	0	0
	R-FR-R	97±1	95±2	93±2	95±1	51±4	9±2	0

* Heat-sensitization was given to the 24-month-aged seeds 4 hr after the beginning of dark period at 20°C.

** Irradiation was given just after transferring to 20°C of germination temperature from high temperature pretreatment after the onset of imbibition.

Fig. 2 Effects of R and GA₃ on germination of the prolonged FR light-irradiated seeds.

A, FR light-irradiation for 48 hr; B, FR irradiation for 144 hr; R, red light; GA₃, gibberellic acid A₃; W, distilled water.

Fig. 3 Effects of R and GA₃ on germination of the heat-sensitized seeds. A, heat-sensitization for 48 hr; B, heat-sensitization for 144 hr; R, red light; GA₃, gibberellic acid A₃; W, distilled water.

exposure to R light before heat-sensitization, but they germinated 93% by 5-min exposure to R light after heat-sensitization (Fig. 3-A). The effects of GA₃ on their germination, however, showed very high percentage regardless of the application before or after heat-sensitization. The heat-sensitized seeds kept at 40°C for 48 hr with 36 and 48 months, on the other hand, did not germinate at all even at the germination temperature of 20°C in darkness or by 5-min exposure to R light before heat-sensitization (Fig. 3-A). The heat-sensitized ones kept at 40°C for 48 hr with 48 months did not germinate more than 23% by 5-min exposure to R light after heat-sensitization or by the application of GA₃, though the heat-sensitized ones kept at 40°C for 48 hr with 36 months germinated 57–84% respectively (Fig. 3-A).

The heat-sensitized seeds kept at 40°C for 144 hr with 24 months after harvest germinated 80–87% respectively by the application of GA₃ before or after heat-sensitization, though they did not germinate at all at 20°C in darkness or germinated only 18% by 5-min exposure to R light after heat-sensitization (Fig. 3-B). The similar heat-sensitized seeds with 36 and 48 months, on the other hand, did not germinate

Table 3 Germination of the seeds which had prolonged exposure to FR light in indicated months after exposure to FR light.

FR* irradiation (hr)	Germination temperature (°C)	Treatment	Germination (%)											
			Months after exposure to FR light**											
			0	3	6	9	12	18	24	30	36			
20	48	Dark	0	86 ± 1	94 ± 3	96 ± 3	92 ± 3	95 ± 2	85 ± 4	79 ± 3	81 ± 2			
		R*** (5-min)	97 ± 1	98 ± 3	94 ± 2	98 ± 1	96 ± 5	96 ± 3	94 ± 4	89 ± 2	93 ± 3			
		GA ₃ 10 ⁻³ M	98 ± 4	97 ± 3	99 ± 1	100	95 ± 2	97 ± 3	96 ± 3	95 ± 5	92 ± 2			
25	48	Dark	0	85 ± 2	92 ± 1	87 ± 3	85 ± 2	90 ± 3	78 ± 5	81 ± 3	72 ± 3			
		R*** (5-min)	98 ± 2	97 ± 2	90 ± 3	93 ± 4	96 ± 3	97 ± 5	86 ± 3	89 ± 5	90 ± 3			
		GA ₃ 10 ⁻³ M	95 ± 1	93 ± 2	100	97 ± 2	98 ± 5	96 ± 4	95 ± 3	97 ± 2	97 ± 3			
20	144	Dark	0	90 ± 3	96 ± 4	89 ± 3	92 ± 1	95 ± 2	96 ± 2	95 ± 3	91 ± 4			
		R* (5-min)	98 ± 2	97 ± 2	95 ± 2	97 ± 1	98 ± 3	97 ± 4	97 ± 4	93 ± 4	96 ± 5			
		GA ₃ 10 ⁻³ M	96 ± 3	97 ± 3	100	97 ± 4	100	96 ± 3	95 ± 5	97 ± 2	95 ± 4			
25	144	Dark	0	92 ± 5	95 ± 3	97 ± 3	91 ± 2	96 ± 2	93 ± 5	92 ± 3	90 ± 2			
		R*** (5-min)	97 ± 3	94 ± 1	93 ± 3	94 ± 5	96 ± 3	95 ± 4	97 ± 2	94 ± 3	97 ± 3			
		GA ₃ 10 ⁻³ M	98 ± 3	97 ± 3	100	97 ± 4	100	96 ± 2	95 ± 5	97 ± 3	96 ± 4			

* Prolonged FR light irradiation was given to the 24-month aged seeds 4 hr after the beginning of dark period at 20 and 25°C.

** The FR light-irradiated seeds were stored at 20°C in darkness for 3, 6, 9, 12, 18, 24, 30 and 36 months.

*** R light irradiation was given 8 hr after the beginning of dark period.

Table 4 Germination of the seeds that had become heat-sensitized in indicated months after heat-sensitization.

Heat (40°C)* Germination sensitization temperature (°C)	Treatment	Germination (%)										
		Months after heat-sensitization**										
		0	3	6	9	12	18	24	30	36		
20	Dark	61 ± 3	88 ± 3	89 ± 2	86 ± 5	85 ± 3	87 ± 4	83 ± 3	78 ± 4	82 ± 4		
	R*** (5-min)	93 ± 3	92 ± 3	95 ± 3	92 ± 4	96 ± 2	93 ± 2	96 ± 5	89 ± 3	94 ± 2		
	GA ₃ 10 ⁻³ M	97 ± 1	94 ± 3	98 ± 2	96 ± 4	96 ± 3	95 ± 5	97 ± 3	97 ± 4	95 ± 3		
25	Dark	43 ± 4	88 ± 2	81 ± 2	85 ± 3	75 ± 4	80 ± 2	79 ± 3	80 ± 4	78 ± 5		
	R*** (5-min)	94 ± 3	92 ± 3	89 ± 2	94 ± 2	91 ± 2	90 ± 4	89 ± 4	91 ± 1	93 ± 4		
	GA ₃ 10 ⁻³ M	94 ± 3	96 ± 1	97 ± 1	90 ± 3	96 ± 3	89 ± 5	95 ± 3	97 ± 2	95 ± 3		
48	Dark	0	0	0	0	0	0	0	0	0		
	R*** (5-min)	18 ± 1	12 ± 2	6 ± 1	8 ± 2	2	1	0	1	1		
	GA ₃ 10 ⁻³ M	87 ± 2	91 ± 3	78 ± 4	67 ± 4	24 ± 4	31 ± 2	19 ± 2	16 ± 3	8 ± 2		
144	Dark	0	0	0	0	0	0	0	0	0		
	R*** (5-min)	0	2	1	2	1	0	0	1	0		
	GA ₃ 10 ⁻³ M	68 ± 3	59 ± 2	12 ± 3	9 ± 3	13 ± 2	9 ± 2	3	2	1		

* Heat-sensitization was given to the 24-month-aged seeds which had been kept in darkness at 20°C after the onset of imbibition.

** The heat-sensitized seeds were stored at 20°C in darkness for 3, 6, 9, 18, 24, 30 and 36 months.

*** R light irradiation was given 8 hr after the beginning of dark period.

at 20°C not only in darkness or by 5-min exposure to R light, but also by the application of GA₃.

Germination in the seeds exposed to the prolonged and 144 FR light or heat-sensitized

The seeds exposed to the FR light for 48 hr after the onset of imbibition germinated 72–97% respectively both at 20 and 25°C in darkness with 3, 6, 9, 12, 18, 24, 30 and 36 months following the exposure to FR light (Table 3) though the seeds have not exposure to FR light, did not germinate at all at 25°C, and did not germinate more than 25% even at 20°C with 60 months after harvest (36 months after the exposure to FR light) (Table 1).

The heat-sensitized seeds kept at 40°C for 48 hr germinated 75–89% both at 20 and 25°C in darkness with 3, 6, 9, 12, 18, 24, 30 and 36 months after heat-sensitization (Table 4). The heat-sensitized ones kept at 40°C for 144 hr, on the other hand, did not germinate at all or a little germinate both at 20 and 25°C in darkness. They, however, germinated 87 and 91% at 20°C, and 59 and 68% at 25°C with 0 and 3 months after the heat-sensitization by the application of GA₃, though they did not germinate more than 18% at 20°C, and did not germinate at all at 25°C by 5-min exposure to R light.

DISCUSSION

The response of seeds toward R and FR lights is influenced by the germination temperature^{2–5,9–14)} and other factors.^{4–12)}

The rate of dark germination of Grand Rapids lettuce seeds was very high at 15°C with 0, 6, 12, 36 and 48 months after harvest, at 20°C with 6, 12, 36 and 48 months, and at 25°C with 6, 12 and 24 months. A brief (5-min) exposure to FR light has also very little influence on germination inhibition (Table 1). Their germination, however, decreased rapidly at 25°C with 48 months, and both 15 and 20°C with 60 months. Danielson and Toole¹³⁾ reported that high temperature imposes a block upon germination beyond that of the active form of phytochrome. The germination of Grand Rapids lettuce seeds at 30°C is induced only by a prolonged exposure to R light more than 16 hr in the fresh seeds and for 1–2 hr in the aged (12 and 24 months) seeds.¹⁰⁾ The germination induction at 30°C, therefore, may occur because the active form of phytochrome becomes functioning to induce germination or overcome blocks other than a direct inactivation of phytochrome system itself by a prolonged exposure to R light more than 16 hr in the fresh seeds and more than 1–2 hr in the aged seeds which were in deteriorating stage.

R light requirement for germination induction in Grand Rapids lettuce seeds is more evident in the dormant and deteriorating stages than in the non-dormant stage if the germination temperature is the same, and is more evident at high temperature than at low temperature if the physiological stage of seeds is the same. FR light requirement for germination inhibition is more evident in the non-dormant stage than in the dormant and deteriorating stages if the germination temperature is the same, and is more evident at low temperature than at high temperature if the physiological stage of the seeds is the same. It is evident that the reversible photoreaction by R and FR lights is regulated not only by the temperature but also by the physiological state of seeds. Ikuma and Thimann⁹⁾ reported that low temperature stimulated lettuce seed germination at a point other than that controlled by phytochrome. Takeba and

Matsubara¹⁴⁾ also explained that the germination of lettuce seeds is regulated not only by the phytochrome system but also by the thermo-labile factors. It is clear that the range of temperature and R light requirement for germination induction or the range of temperature and FR light requirement for germination inhibition changed with the physiological state of seeds. Grand Rapids lettuce seeds have been generally classified as the light-sensitive simply because their full germination occurs at 20 and 25°C in light, but they become light-insensitive by after-ripening and behave in a similar way to the classically light-insensitive Great Lakes, and become light-sensitive again in the deteriorating stage.

The germination induction and the sensitivity to R light and GA₃ in the seeds exposed to FR light did not decrease with the passage of time after the prolonged exposure to FR light. Their germination rate showed a higher percentage than in the seeds which had not prolonged exposure to FR light with 60 months after seed harvest (36 months after the prolonged exposure to FR light) (Tables 1 and 3). It can therefore be said that the photoreversible induction or germination inhibition in the seeds exposed to FR light are due to the change from the non-dormant stage to the secondary photo-dormant stage. The photoreversible induction or germination inhibition in the heat-sensitized seeds, on the other hand, can be divided into two distinct physiological states. The germination induction and the sensitivity to R light and GA₃ in the heat-sensitized seeds kept at 40°C for 48 hr did not decrease with the passage of time after heat-sensitization. Their germination rate showed a high percentage both at 20 and 25°C as the same as that of the seeds exposure to FR light (Tables 3 and 4). It can therefore be said that the photoreversible induction or germination inhibition in the heat-sensitized seeds kept at 40°C for 48 hr are due to the change from the non-dormant stage to the secondary thermo-dormant stage. The heat-sensitized seeds kept at 40°C for 144 hr, on the other hand, are led from the non-dormant stage to the deteriorating stage caused by the thermal injury. This is because they did not show any germination both at 20 and 25°C in darkness with 0–36 months after heat-sensitization (Table 4).

They also did not show more than 18% at 20°C and 2% at 25°C by 5-min exposure to R light with 0–36 months after heat-sensitization. They, however, germinated 87 and 91% at 20°C, and 59 and 68% at 25°C by the application of GA₃ with 0 and 3 months after heat-sensitization, though they did not germinate more than 8% with 36 months after it (60 months after seed harvest) (Table 4).

The seed dormancy means a state in which the germination is temporarily suspended under favorable and unfavorable temperature, or the cessation of growth in the embryo without losing and reducing its viability for prolonged time.¹⁵⁾ Grand Rapids lettuce seeds in the deteriorating stage have decreased in tolerance to sub-optimal temperature in germination and increased in sensitivity to R light, GA₃ and thiourea.¹⁰⁾ With the further progress of deterioration, they decreased tolerance to optimal temperature and sensitivity to R light, GA₃ and thiourea.

R light irradiation given to lettuce seeds increased the growth potential of the embryonic axes, and overcame the mechanical restraint imposed by the endosperm coat.^{4,16)} The increase in the growth potential of the embryo axes during imbibition has been shown to be closely related to the accumulation of free amino acids (especially Gln* and Glu**) in the axes¹⁷⁾ and with the GS*** activity in the axes.¹⁸⁾ The

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* Gln: Glutamine, ** Glu: Glutamic acid, *** GS: Glutamine synthetase.

GS activity increased by the R light and GA_3 , but FR light given immediately after the R light cancelled the GS activity, and R light given immediately after the FR light increased again the GS activity.¹⁹⁾ It is reported further that the GS activity decreased rapidly during imbibition at 35°C, but not at 18°C. The germination inhibition in the lettuce seeds caused by the prolonged exposure to FR light or high temperature pretreatment at 40°C for 48 hr after the onset of imbibition may inhibit temporarily the GS activity in their embryonic axes. The inhibition or decrease of their GS activity, however, may release or increase with the passage of time after heat-sensitization, because they germinated 78–89% at 20°C and 75–88% at 25°C with 3–36 months, though they did not germinate more than 61% at 20°C and 43% at 25°C with 0 month after heat-sensitization (Table 4).

The induction effects of germination in the heat-sensitized seeds kept at high temperature after the onset of imbibition are greater in GA_3 than in R light, and at 20°C than at 25°C (Table 4). It may be considered that the seeds which are aged 24 months and heat-sensitized at 40°C for 144 hr have two different germination pathways at least; the R light dependent pathway and the GA_3 dependent one. The R light dependent pathway may be broken by heat-sensitization at 40°C for 144 hr, because they did not germinate at all or a little germinate both at 20 and 25°C (Fig. 3-B and Table 4). It may also be said that the two different germination pathways in the heat-sensitized seeds which are R light and GA_3 dependent are due to the difference of the GS activity caused by R light and GA_3 , though the effects of GA_3 on GS activity was very similar to that of R light.²⁰⁾

The difference in germination induction by 5-min exposure to R light or by the application of GA_3 between the heat-sensitized seeds which were aged 24 months and those aged 36 and 48 months is due to the difference in the physiological state of seeds. It can be said that the seeds aged 36 and 48 months are in the initial phase of deteriorating stage, because the germination in the seeds aged 36 months began to decrease at 25°C in darkness even without heat-sensitization, though they showed high percentage germination at 20°C (Table 1 and Fig. 3).

Our findings may be summarized into the following scheme (Fig. 4) by adding to them a part of previous reports by Suzuki et al.⁹⁾ and Suzuki.¹⁰⁾

A_1 is the dormant stage without after-ripening, A_2 is the non-dormant stage which had become non photoreversible at 15, 20 and 25°C by after-ripening, and A_3 is the deteriorating stage which starts after the non-dormant stage which had become photoreversible again. $A_1 \rightarrow A_2$ is the period of after-ripening, and it can also be called the dormancy releasing period. $A_2 \rightarrow A_3$ is the period proceeding to the deteriorating stage which is leading to the decrease in germination velocity and the loss of viability with the progress of ageing. With the further progress of ageing, they do not germinate by the exposure to R light or GA_3 . $A_2 \rightarrow A_3$ stage should not be included in the period of after-ripening, because the period of after-ripening is referred to as a dormant or rest period. $A_2 \rightarrow A_2'$ is changed to the secondary photo-dormant stage caused by the prolonged exposure to FR light. $A_2 \rightarrow A_2''$ is changed to the secondary thermo-dormant stage caused by heat-sensitization at 40°C for 48 hr, because the seeds in that stage do not lose or reduce its viability for a prolonged time, though their germination is temporarily suspended under favorable and unfavorable temperature. $A_2 \rightarrow A_2'''$ is changed to the deteriorating stage caused by heat-sensitization at 40°C for 144 hr, which leads to the decrease in germination velocity and the loss of viability by high temperature pretreatment after the onset of imbibition.

Fig. 4 A model of germination induction in the seeds of Grand Rapids lettuce. A₁, dormant stage; A₂, non-dormant stage; A₂', secondary photo-dormant stage; A₂'', secondary thermo-dormant stage; A₂''', deteriorating stage by high temperature pretreatment; A₃, deteriorating stage; R, red light; FR, far-red light; HT, high temperature pretreatment; B, precursors; GER, germination.

A₁→B, A₂'→B, A₂'→B, A₂'→B and A₃→B depend upon the active form of phytochrome or GA₃ except at 30°C. A₂'→B and A₂'→B, furthermore, become independent of the active form of phytochrome or GA₃ due to the releasing of secondary photo- or thermo-dormancy.

To discuss the so-called high energy reaction by the prolonged exposure to FR light or the physiological nature in the dormant, secondary photo- or thermo-dormant and deteriorating seeds further detailed study will be required.

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〈和文抄録〉

Grand Rapids レタス種子発芽の光および温度制御に及ぼす age の影響

鈴木 善弘

福島大学教育学部

Grand Rapids レタス種子の発芽に及ぼす赤色光 (red light), 遠赤色光 (far-red light) による光可逆的反応は, 発芽温度のみならず age の進行によっておこる種子の生理的状态によって著しく異なり, 非休眠過程の種子よりも, 休眠および発芽力消失過程の種子においてより明らかである。

遠赤色光 (far-red light) を長時間照射した種子, あるいは高温 (40°C) で 48 時間処理した種子は, 照射しない種子あるいは高温処理を行わない種子より発芽速度の低下もおそく, 発芽能力が長く保持される。

光可逆性を失った非休眠種子の発芽に対する長時間の遠赤色光 (far-red light) 照射による光可逆性の再誘導は光による二次休眠の誘導であるが, 高温処理による光可逆性の再誘導は非休眠種子を異なった二つの生理的状态へ誘導する。その一つは, 48 時間の高温 (40°C) 処理による二次休眠の誘導であり, 他の一つは 144 時間の高温 (40°C) 処理による発芽力の消失過程への誘導である。

高温処理によって誘導された発芽力消失の生理的状态にある種子の発芽に対する GA₃ の効果は赤色光 (red light) より大きい。