Plant Physiol. (1981) 67, 1224–1229
0032-0889/81/67/1224/06/$00.50/0

Factors Affecting the Induction of Secondary Dormancy in Lettuce[1]

Received for publication September 19, 1980 and in revised form December 16, 1980

DAVID N. KRISTIE, PAWAN K. BASSI AND MARY S. SPENCER
Department of Plant Science, University of Alberta, Edmonton, Alberta, Canada T6G 2P5

ABSTRACT

The relationship between the temperature at which germination of 50% of the seeds is inhibited in the light (GT_{50} Light) and secondary dormancy was investigated in three cultivars of *Lactuca sativa* L. Seeds were incubated for varying periods under non-germinating conditions and subsequent germination in response to red light (R) was determined over a wide range of temperatures. Dark incubation at 32 C reduced the GT_{50} Light of cv. New York but did not affect germination at temperatures below 24 C. Dark, 32 C incubation had no effect on the GT_{50} Light of cv. Great Lakes. In cv. Grand Rapids, dark incubation at 15, 24, 32, or 35 C initially reduced the GT_{50} Light. However, longer incubations induced a secondary dormancy, *i.e.*, the seeds became unable to germinate at all temperatures in response to R given after the high temperature incubation. A single exposure to R at the beginning of a 32 C incubation slowed the induction of secondary dormancy. Repeated exposures to R prevented the induction of secondary dormancy, but did not prevent a decline in the GT_{50} Light. GA_3 mimicked the effect of repeated R.

The differences in the germination behavior of the three cultivars suggest that there may be qualitative differences in the germination mechanism of these cultivars. This research demonstrates the significance of monitoring germination at a range of temperatures to avoid misinterpretation of the data.

Lettuce (*Lactuca sativa* L.) seed germination is strongly temperature dependent. As the temperature rises above the optimum (18), germination declines sharply, often falling from 100% to near 0% with an increase of only 2 or 3 degrees C (23). The temperature at which there is a 50% reduction in germination has been termed as upper temperature cut-off point (31) or simply, GT_{50} (10). When seeds are exposed to temperatures above GT_{50}, they become thermodormant. In lettuce, GT_{50} typically occurs in the range of 25 to 30 C, but the precise temperature may differ among cultivars (24, 32), and among different lots of the same cultivar (26).

Numerous studies have shown that the promotive or inhibitory effects of chemical or physical factors on germination can be related to shifts in the GT_{50} (11, 12, 20–24). A brief exposure to R[2] raises the GT_{50} in both light sensitive (*e.g.* Grand Rapids) and so-called light insensitive cultivars such as Great Lakes (11, 20). For descriptive purposes, lettuce may be thought of as having two GT_{50}, one for germination in the dark (GT_{50} Dark) and one for germination in the light (GT_{50} Light) (20). The germination-modifying effects of GA_3, KIN, AbA, and solutions of high osmotic pressure have been shown to be related to changes in one or both of these GT_{50} (21, 24).

Incubation of fully imbibed seeds under conditions not suitable for germination is known to reduce their germination potential. High temperature incubations can induce a light requirement in dark germinating lettuce seeds (1, 2), *i.e.*, the seeds become photodormant. This effect has been attributed to a decline in the GT_{50} Dark (11, 12). In the light sensitive cv. Grand Rapids, prolonged dark, or high temperature incubations may also decrease photosensitivity until the seeds become unresponsive to R, *i.e.* secondarily dormant (3, 4, 9, 27, 31, 34, 35).

In most previous studies of secondary dormancy, its onset has been monitored at only one temperature, thus, little is known about the changes in GT_{50} Light during the induction of secondary dormancy. In the present study, changes in germination have been monitored over a wide range of temperatures in the examination of the effects of interactions among light, temperature and growth regulators on the induction of secondary dormancy in three lettuce cultivars.

In this paper, high-temperature incubation refers to the lowest temperature capable of suppressing germination to zero in both light and dark treatments; and secondary dormancy refers to the seeds that become incapable of germination in response to R at any temperature.

MATERIALS AND METHODS

Plant Materials. Achenes of *L. sativa* L. cvs. Grand Rapids (lot I), New York, and Great Lakes were obtained from the Robertson Seed Co., Edmonton, Alberta. Another lot of Grand Rapids (lot II) was obtained from the Carolina Biological Supply Co., Gladstone, OR. All seeds were examined before use and damaged, abnormally small, or off-color seeds were discarded.

Germination Studies. For each replicate approximately 100 seeds were distributed in 9-cm plastic Petri dishes containing 2 layers of Whatman No. 1 filter paper and 5 ml distilled H_2O or test solution. Seeds were incubated under non-germinating conditions provided by darkness or supraoptimal temperatures, depending on the cultivar. High temperature incubations were conducted at the lowest temperature capable of suppressing germination to 0% under both light and dark germination conditions. This was 35 C for cv. Grand Rapids (I) and 32 C for all other seed lots (Table I). For dark incubations Petri dishes were wrapped in a single layer of aluminum foil. In some experiments seeds were exposed to R during the course of a high temperature incubation. In these cases the Petri dishes were sealed with parafilm to prevent them from drying out. At the end of the incubation period all Petri dishes were opened to room air and any seeds that had germinated were removed. Following a light or hormone treatment all samples were wrapped in aluminum foil and placed in growth cabinets adjusted to temperatures of 15, 20, 22, 24, 26, 28, 30, 32 or 35 C. Temperatures within the Petri dishes were measured with a copper/constantan thermocouple and were found to vary less

[1] This work was supported by the Natural Sciences and Engineering Research Council of Canada grant (A-1451) to MS in aid of this research and a Postgraduate Scholarship for DK.

[2] Abbreviations: R, red light; FR, far red light; KIN, kinetin.

than ± 0.25 C. Germination, as measured by radicle emergence, was determined after 5 days in cv. Great Lakes. In all other seed lots germination was determined after 3 days in seeds kept at 20 to 35 C, and after 5 days in seeds at 15 C. No further germination occurred after these times. All treatments were represented by at least three replicates. Most experiments were repeated at least once.

Light Sources. All manipulations of the seeds were conducted in a darkroom under a green safelight consisting of two 15-w cool-white fluorescent tubes wrapped in a triple layer of No. 39 'primary green' Cinemoid (Rank Strand Electric Ltd., London, England). Red irradiation (7.5×10^{18} $Q \cdot m^{-2} \cdot s^{-1}$) was provided by filtering the light from four 15-w cool-white fluorescent tubes through a double layer of No. 15 'ruby' Cinemoid. Far red light (1.1×10^{18} $Q \cdot m^{-2} \cdot s^{-1}$) was obtained by filtering the light of four 75-w incandescent bulbs through 10 cm water and one layer each of No. 5 'orange' and No. 20 'deep blue' Cinemoid. All light treatments were for 5 min.

RESULTS

Preliminary Experiments. Seeds of three different lettuce cultivars were imbibed at temperatures ranging from 20 to 35 C either in light or darkness (Table I). At 20 C, the seeds of cvs. Grand Rapids (II) and New York were light-sensitive as compared to cvs. Grand Rapids (I) and Great Lakes that germinated fully in both light and dark. In all seed lots, as temperatures increased, dark germination levels declined more rapidly than germination in response to R. Thus at 30 C, R promoted germination even in the so-called light insensitive cultivar, Great Lakes. Similar results have been obtained by other workers (29).

In another experiment, the effects of high temperature incubation (35 C) on the germination of cv. Grand Rapids (I) in the dark, or after exposure to R, were examined (Figs. 1 A and B). High temperature incubations progressively suppressed subsequent dark germination at all temperatures ranging from 15 to 26 C. Germination in response to R was also severely suppressed at 24 and 26 C. Both the GT_{50} Dark and the GT_{50} Light declined during high temperature incubation. The seeds became photodormant at 15 and 20 C while simultaneously becoming unresponsive to R at 24 and 26 C. These results demonstrate the importance of conducting germination studies over a wide range of temperatures. In the earlier reports, when after exposure to high temperatures the subsequent germination was monitored only at one temperature, high temperature incubations of less than 24 h were often found to have no effect on the germination of Grand Rapids seeds, in response to R (5, 35). The dangers of monitoring germination at a single or a few arbitrarily chosen temperatures have been stressed by Reynolds (20). In all further experiments germination was determined at eight temperatures ranging from 15 to 32 C.

Table I. *The Influence of Light and Temperature on the Germination of Several Varieties of Lettuce*

Seeds were imbibed 1 h at 22 C before light treatment and transferred to the indicated temperatures. Germination was determined after 48 h. Each value represents the mean of 2 samples.

Variety	Light Conditions	% Germination				
		Germination temperature (C)				
		20	26	30	32	35
Grand Rapids (I)	R	100	100	85	25	0
	D	100	68	17	0	0
Grand Rapids (II)	R	100	100	20	0	0
	D	23	0	0	0	0
Great Lakes	R	100	100	52	0	0
	D	100	100	1	0	0
New York	R	94	97	47	0	0
	D	60	38	0	0	0

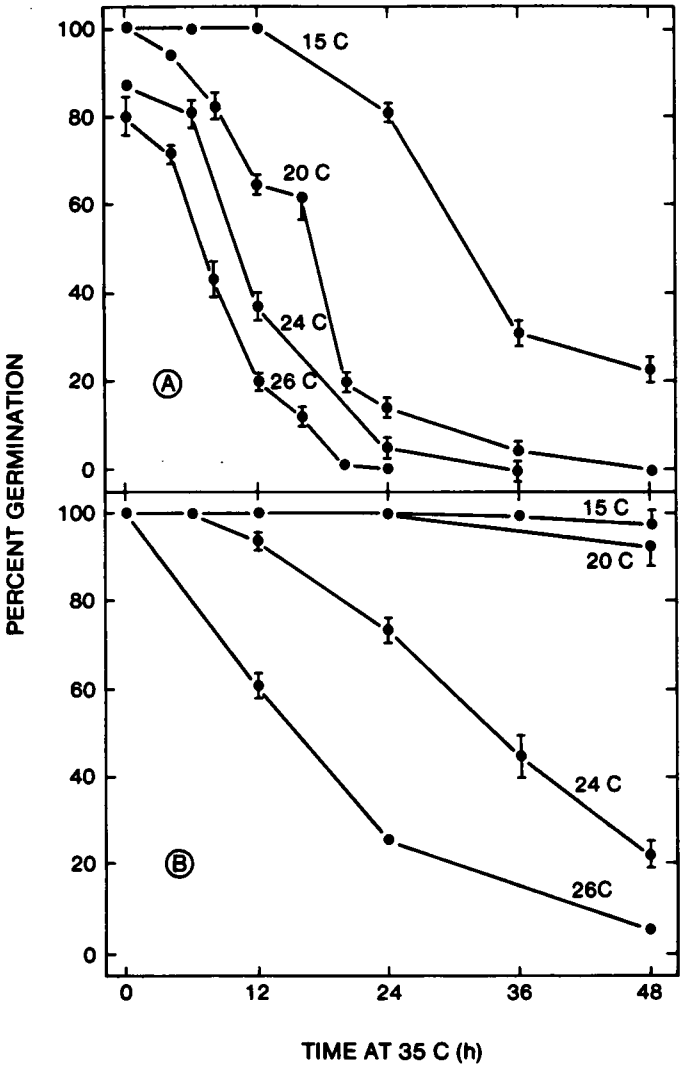

FIG. 1. Effects of high temperature incubation on the subsequent germination of dark or R treated seeds. Seeds of cv. Grand Rapids (I) were incubated in the dark at 35 C for varying periods and transferred directly to the indicated temperatures (A) or were exposed to R before transfer (B). Each point represents the mean of 3 samples. The treatments can be summarized as follows: Preincubation (0 to 48 h) at 35 C → R (5 min) → Incubation at 15 to 26 C.

Response of Different Cultivars to High Temperature Incubation. The effects of high temperature incubations on the GT_{50} Light of three lettuce cultivars are shown in Figure 2. Prolonged incubations had little effect on the GT_{50} Light of cv. Great Lakes. In contrast, both cv. New York and cv. Grand Rapids showed considerable declines in their GT_{50} Light, particularly within the first 0.5 days of incubation. Two days of incubation reduced the GT_{50} Light of cv. New York to approximately 25 C; longer incubations had little further effect on the GT_{50} Light. In cv. Grand Rapids (I), incubations longer than 1 day reduced germination at all temperatures and eventually led to the total suppression of germination. After 8 days of high temperature incubation, GT_{50} Light in cv. New York was 24.5 C as compared to 28.5 C in cv. Great Lakes. In cv. Grand Rapids (I), germination declined to below 20% after 8 days of high temperature incubation. Repeated or prolonged exposures to R had no additional effect on germination in any cultivar. Prolonged high temperature incubations

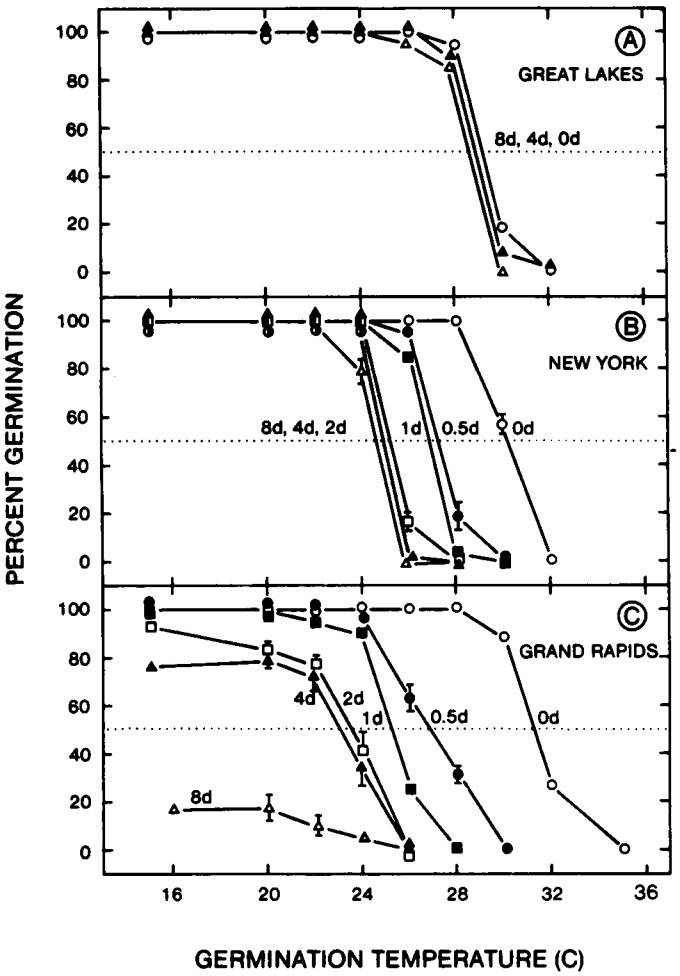

FIG. 2. Effects of high temperature incubation on the GT_{50} Light of cv. Great Lakes, New York, and Grand Rapids (I). Seeds were incubated at 32 C (Great Lakes, New York) or 35 C (Grand Rapids [I]) for periods of 0.5 to 8 days, exposed to R and transferred to the indicated temperatures. Untreated seeds (Od) were imbibed 1 h at 24 C before R irradiation and then transferred to germination temperatures. Each point represents the mean of 4 samples. The treatments can be summarized as follows: Preincubation (0 to 8 days) at 32 or 35 C → R (5 min) → Incubation at 15 to 35 C.

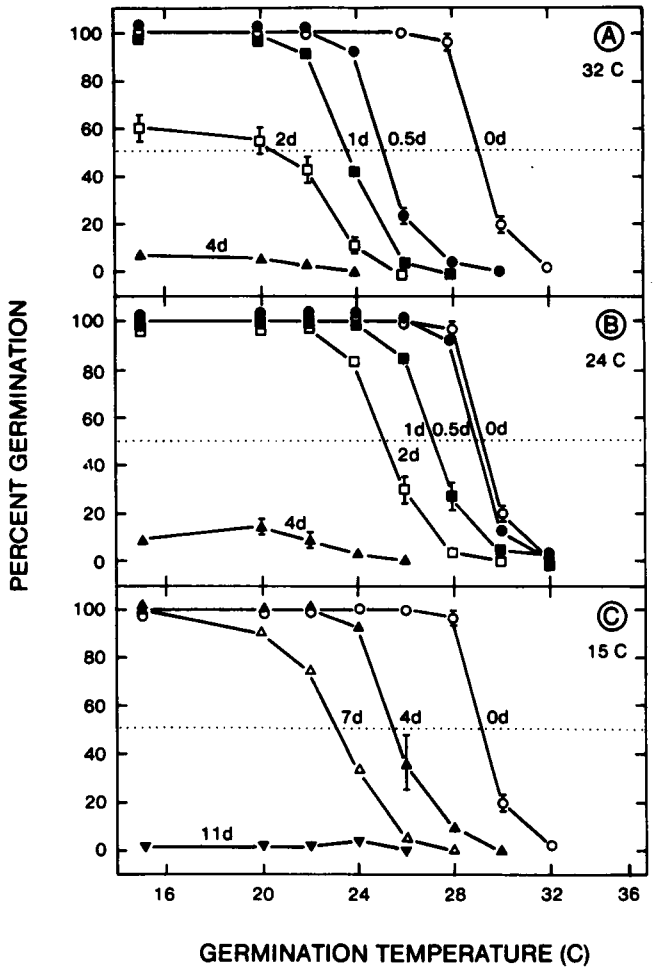

FIG. 3. Effects of dark incubation at 32, 24, or 15 C on the GT_{50} Light of cv. Grand Rapids (II). The procedure was the same as in Figure 2 except dark incubations were at 32, 24, and 15 C. For untreated seeds (Od) each point represents the mean of 10 samples. All other points represent the mean of 4 samples. The treatments can be summarized as follows: Preincubation (0–11 days) at 32, 24 or 15 C → R (5 min) → Incubation at 15 to 32 C.

also affected the time course of germination. Eight days of high temperature incubation delayed emergence by up to 24 h in all three cultivars.

Effect of Incubation Temperature on Dormancy Induction. The effect of incubation temperature on the rate and pattern of dormancy induction in cv. Grand Rapids (II) is shown in Figure 3. Dark germination was less than 5% at all incubation temperatures. The decline in GT_{50} Light was temperature dependent. Twelve h at 32 C reduced the GT_{50} Light to approximately 25 C. Two days at 24 C and 4 days at 15 C caused a similar decline in the GT_{50} Light. Dormancy induction appeared to occur in two stages at all three incubation temperatures. Initially, germination was reduced only in the vicinity of the GT_{50} Light; longer incubations eventually suppressed germination at all temperatures.

The complete suppression of germination occurred more rapidly in lot II (Fig. 3 B) than in lot I of cv. Grand Rapids (Fig. 2 C). This was true even when lot II was incubated at much lower temperatures (24 C, as compared to 35 C for lot I). Within the same seedlot the rate of dormancy induction was temperature dependent, being more rapid at higher incubation temperatures.

Role of Light and Growth Regulators. Secondary dormancy can usually be broken by a combination of R plus growth regulators such as KIN, ethylene or GA_3 (7, 27, 28, 34, 35). In our own experiments, a higher level of germination could be restored in secondarily dormant seeds by R + KIN than by R + GA_3 (Fig. 4). In the absence of R, neither GA_3 or KIN had any promotive effect on germination (data not shown).

In all the experiments discussed above, secondary dormancy was induced by dark incubation. To determine the effect of light on the induction of secondary dormancy, seeds were exposed to R during the course of a high temperature incubation (Fig. 5). Compared to the dark incubation control, both initial R and repeated R treatments slowed the decline in the GT_{50} Light. Prolonger high temperature incubations eventually suppressed germination at all temperatures in seeds receiving a single exposure to R (initial R) but not in seeds receiving repeated exposures to R (repeated R). Previous reports (*e.g.* 33) and data presented in Figure 6 indicate that the promotive effects of a single exposure to R are completely lost within 48 h at high temperatures, presumably through the thermal reversion and/or destruction of Pfr. To determine if the escape reactions of the phytochrome system were involved in prevention of the second stage of dormancy induction, seeds receiving repeated R were exposed to FR instead of R at the end of the high temperature incubation. Zero germination oc-

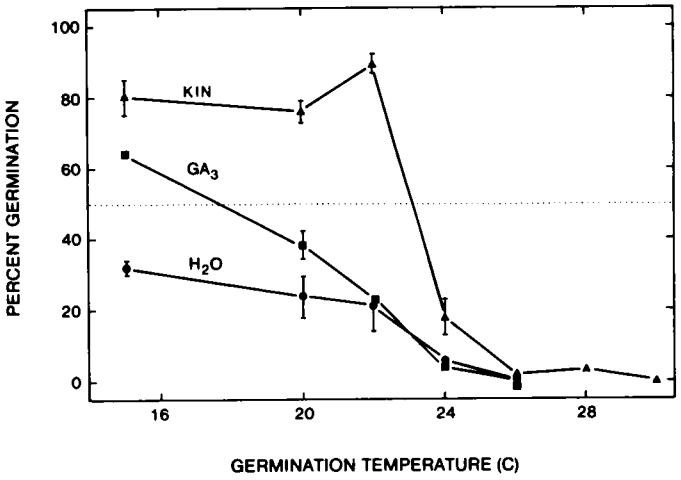

FIG. 4. Germination of secondarily dormant seeds in response to KIN or GA_3. Seeds of cv. Grand Rapids (II) were incubated for 4 days at 32 C and transferred to fresh Petri dishes containing distilled H_2O, 100 μg/ml GA_3 or 10 μg/ml KIN. All samples were then exposed to R and transferred to the indicated temperatures. Each point represents the mean of 4 samples. The treatments can be summarized as follows: Preincubation (4 days) at 32 C → H_2O, GA_3 or KIN → R (5 min) → Incubation at 15 to 30 C.

curred at all temperatures (15 to 32 C) regardless of the length of the incubation period (0.5, 1, 2, 4 days) (data not shown). Thus escape from FR reversibility did not occur since Pfr was still required to promote germination after transfer to germination temperatures.

Gibberellic acid is known to promote the germination of photodormant lettuce seeds (14). Seeds were imbibed in GA_3 during the course of a 4-day high temperature incubation to determine if GA_3 could substitute for repeated R in preventing the induction of secondary dormancy. Previous results had indicated that R + GA_3 applied after a high temperature incubation promoted the germination of secondarily dormant seeds (Fig. 4). GA_3 is as effective as repeated R in preventing the second stage of dormancy induction (Fig. 7).

DISCUSSION

Secondary dormancy is known to occur in a number of light sensitive species, for example, *Chenopodium album* L., *Rumex crispus* L. and *L. sativa* L. (3, 15, 32). In lettuce, secondary dormancy has been reported in cv. Grand Rapids, and several European cultivars. Some cultivars appear to be immune to the induction of secondary dormancy (32). From the present study it is clear that if the term secondary dormancy is reserved for those seeds that become unable to germinate at any temperature in response to R, then only cv. Grand Rapids became secondarily dormant. High temperature incubations reduced the GT_{50} Light of cv. New York, however.

The difference in germination behavior between Grand Rapids and Great Lakes 'type' cultivars is thought to be quantitative, rather than qualitative, with respect to temperature (8). The fact that secondary dormancy can be induced in some cultivars but not in others suggests that there may be qualitative differences among the germination mechanisms of these cultivars. One possible difference that deserves further study relates to the effects of supraoptimal temperatures on the phytochrome system. Our results and earlier studies (13, 25) indicate that the escape reactions of the phytochrome system do not proceed to completion in seeds of cv. Grand Rapids held at high temperatures (above 30 C). In contrast, Negm *et al.* (19) clearly showed that escape from FR reversibility does occur at 35 C in cv. Great Lakes (Mesa 659). The reason for these conflicting results is not readily apparent.

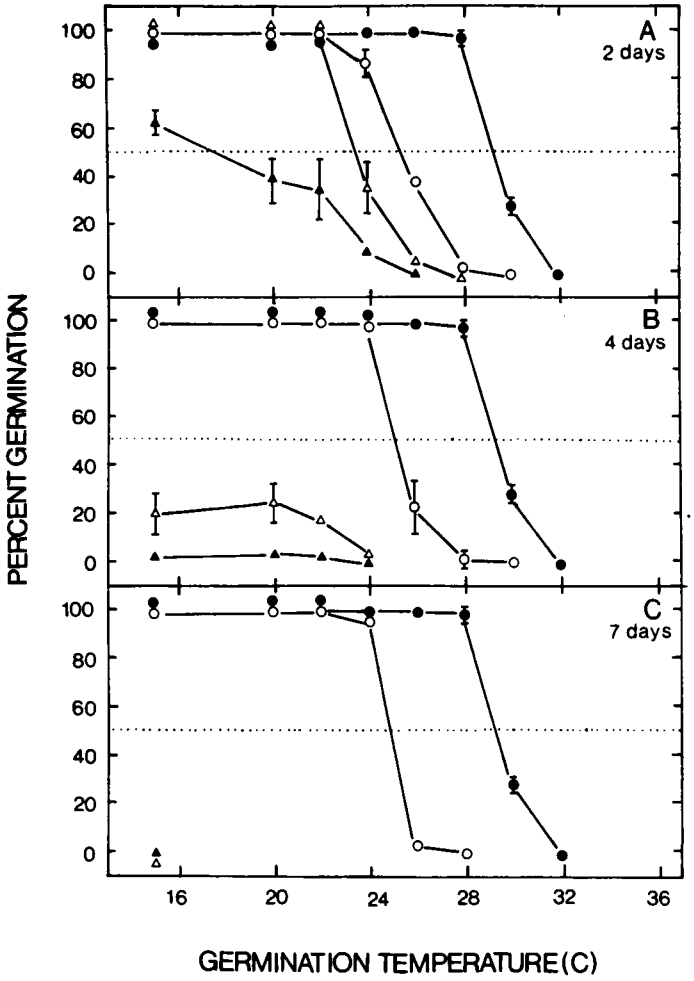

FIG. 5. Effect of light on the induction of secondary dormancy. Seeds of cv. Grand Rapids (II) were incubated at 32 C for 2, 4, or 7 days under varying light conditions; initial R (5 min R), 1 h after the start of imbibition (△); repeated R (5 min R) every 30 min throughout the incubation period (○); Dark (▲). At the end of the 32 C incubation all seeds were exposed to R and transferred to the indicated temperatures. A control treatment (●) was imbibed 1 h at 24 C, before R irradiation and transferred to the indicated temperatures. Each point represents the mean of 4 samples. The treatments can be summarized as follows: Preincubation (R or Dark) (2, 4 or 7 days) at 32 C → R (5 min) → Incubation at 15 to 32 C.

The induction of secondary dormancy in cv. Grand Rapids appeared to occur in two stages, *i.e.* a decline in the GT_{50} Light, followed by the suppression of germination at all temperatures. Exposing seeds to R or GA_3 during the course of a high temperature incubation prevented the second stage of dormancy induction, but did not prevent a decline in the GT_{50} Light. This fact, combined with the observation that high temperature incubation reduced the GT_{50} Light of cv. New York without inducing secondary dormancy, suggests that separate processes may control the two stages of dormancy induction. The present data do not rule out the possibility that these two stages of dormancy induction are the result of the same or similar processes carried to different degrees of completion.

The two stages of dormancy induction resemble the 'toxic' and 'inhibitory' effects of germination inhibitors on lettuce seed, described by Reynolds (21, 22). Extremes of pH reduced germination at all temperatures, an effect described as toxic. Low concentrations of AbA suppressed germination by reducing the GT_{50}. This was termed 'true' inhibition. The suppression of germination by AbA involved both effects, with AbA being inhibitory at low

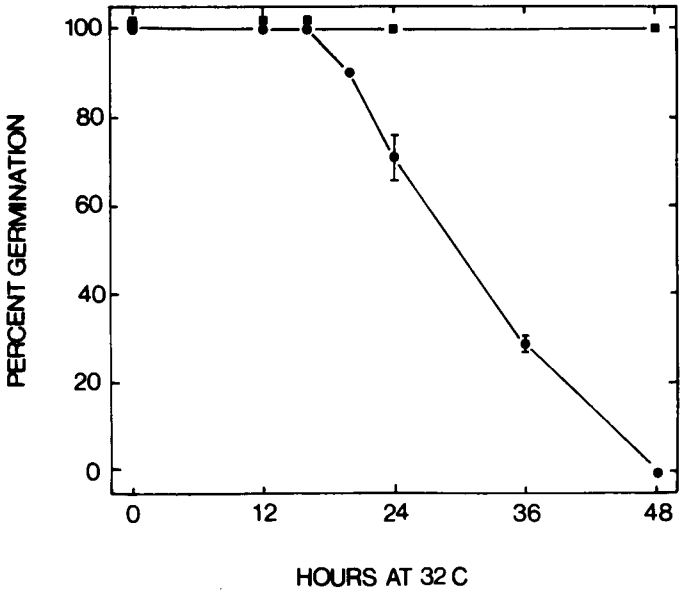

FIG. 6. Reversal of R-promoted germination, by incubation at 32 C. Seeds of cv. Grand Rapids (II) were imbibed 1 h at 20 C before R irradiation and transferred to 32 C. After varying durations of 32 C incubation, the seeds were transferred directly to 20 C (●) or were exposed to R before transfer to 20 C (■). Each point represents the mean of 4 samples. The treatments can be summarized as follows: Imbibition at 20 C (1 h) → R (5 min) → Preincubation (0 to 48 h) at 32 C → R (5 min) → Incubation at 20 C.

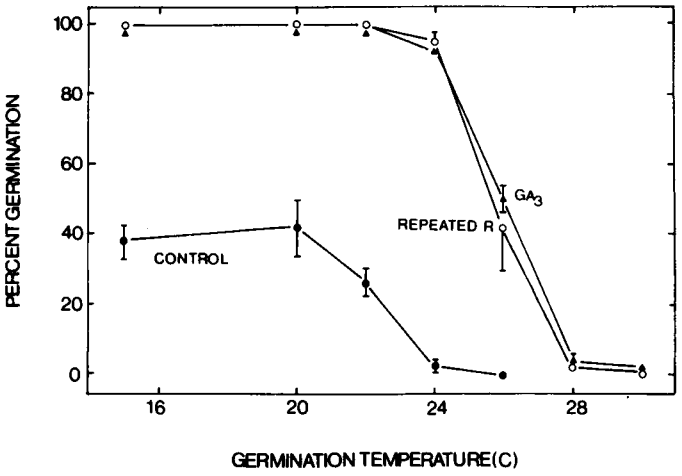

FIG. 7. Effect of GA_3 on the induction of secondary dormancy. Seeds of cv. Grand Rapids (II) were incubated for 4 days at 32 C in 100 μg/ml GA_3 or under repeated R conditions. The control treatment consisted of dark incubation in water. Following 32 C incubation, all samples were exposed to R and transferred to 100 μg/ml GA_3. Germination was determined at the indicated temperatures. Each point represents the mean of 3 samples. The treatments can be summarized as follows: Preincubation (4 days) (GA_3, R or H_2O) at 32 C → R (5 min) → Incubation (GA_3) at 15 to 30 C.

concentrations, but becoming toxic at high concentrations. The pattern of dormancy induction observed here is compatible with the hypothesis that secondary dormancy reflects the accumulation of an inhibitor such as Aba (27).

The ability of GA_3 and Pfr (or its products) to prevent the induction of secondary dormancy has not been previously reported. Khan and Karssen (17) found that R or a combination of KIN, ethephon and GA_{4+7} prevented the induction of a secondary light requirement (*i.e.* prevented photodormancy) in seeds of cv. Great Lakes and Grand Rapids incubated at high temperatures. Vidaver and Hsiao (35) concluded that the induction of secondary dormancy in cv. Grand Rapids was independent of the phytochrome status of the seed. However, their study failed to take into account the rapid thermal reversion and/or destruction of Pfr that occurs in seeds held at high temperatures (33). The induction of secondary dormancy occurred more rapidly in lot I of Grand Rapids than in lot II. This probably relates to the fact that Lot I exhibited a high level of dark germination at temperatures up to 26 C (Fig. 1), while dark germination levels were negligible in lot II at all temperatures above 15 C. Presumably, Pfr levels are higher in dark germinating seeds.

The induction of secondary dormancy appears to involve an effect on the phytochrome system itself. In lettuce cv. Grand Rapids (13), *R. crispus* L. (6, 30) and *C. album* L. (16), prolonged dark incubations decrease photosensitivity until all three species become unresponsive to R, or secondarily dormant. The induction of secondary dormancy in *R. crispus* did not affect phytochrome transformations, or appear to involve a decrease in total phytochrome. In lettuce, Pfr is present in secondarily dormant seeds exposed to R, but it cannot function to promote germination unless a growth regulator such as KIN is also present (27, 28). Duke *et al.* (6) concluded that the decline in photosensitivity and eventual imposition of secondary dormancy in *R. crispus* was related to decreased levels of 'X', the component with which Pfr interacts. If this is the case then the protective effect of R or GA_3 could involve preventing the loss or disorganization of the X factor.

LITERATURE CITED

1. BORTHWICK HA, SB HENDRICKS, MW PARKER, EH TOOLE, VK TOOLE 1952 A reversible photoreaction controlling seed germination. Proc Natl Acad Sci USA 38: 662–666
2. BORTHWICK HA, SB HENDRICKS, EH TOOLE, VK TOOLE 1954 Action of light on lettuce seed germination. Bot Gaz 115: 205–225
3. BURDETT AN 1972 Antagonistic effects of high and low temperature pretreatments on the germination and pregermination ethylene synthesis of lettuce seeds. Plant Physiol 50: 201–204
4. BURDETT AN 1972 Ethylene synthesis in lettuce seeds: its physiological significance. Plant Physiol 50: 719–722
5. CARPITA NC, MW NABORS 1976 Effect of 35 C heat treatments on photosensitive Grand Rapids lettuce seed germination. Plant Physiol 57: 612–616
6. DUKE SO, GH EGLEY, BJ REGER 1977 Model for variable light sensitivity in imbibed dark-dormant seeds. Plant Physiol 59: 244–249
7. DUNLAP JR, PW MORGAN 1977 Reversal of induced dormancy in lettuce by ethylene, kinetin and gibberellic acid. Plant Physiol 60: 222–224
8. EVANARI M 1961 A survey of the work done in seed physiology by the Dept. of Botany, Hebrew University, Jerusalem. Proc Int Seed Test Assoc 37: 865–880
9. GUTTERMAN Y, M EVANARI, W HEYDECKER 1972 Phytochrome and temperature relations in *Lactuca sativa* L. cv. Grand Rapids germination after thermodormancy. Nature New Biol 235: 144–145
10. HEGARTY NW, HA ROSS 1979 Effects of light and growth regulators on germination and radicle growth of lettuce seeds held under high-temperature stress and water stress. New Phytol 82: 49–57
11. HEYDECKER W, A JOSHUA 1976 Delayed interacting effects of temperature and light on the germination of *Lactuca sativa* seeds. Seed Sci Technol 4: 231–238
12. HEYDECKER W, A JOSHUA 1977 Alleviation of thermodormancy of lettuce (*Lactuca sativa* L.). Hort Sci 52: 87–98
13. IKUMA H, KV THIMANN 1964 Analysis of germination processes of lettuce seed by means of temperature and anaerobiosis. Plant Physiol 39: 756–767
14. KAHN A, JD GASS, OE SMITH 1957 Effect of gibberellin on germination of lettuce seeds. Science 125: 645–646
15. KARSSEN CM 1967 Light promoted germination of the seeds of *Chenopodium album* L., I. The influence of the incubation time on the quantity and rate of response to red light. Acta Bot Neerl 16: 156–160
16. KARSSEN CM 1970 The light promoted germination of the seeds of *Chenopodium album* L. IV. Effect of red, far red, and white light on non-photoblastic seeds incubated in mannitol. Acta Bot Neerl 19: 95–108
17. KHAN AA, CM KARSSEN 1979 Photo and hormonal regulation of secondary dormancy in *Lactuca sativa* L., *Apium graveolens* L. and *Chenopodium bonus-henricus* L. seeds. Abstracts Tenth Int Congr on Plant Growth Substances, p 24
18. MAYER AM, A POLJAKOFF-MAYBER 1975. The Germination of Seeds. Pergamon Press, Oxford
19. NEGM FB, OE SMITH, J KUMAMOTO 1973 The role of phytochrome in interaction with ethylene and carbon dioxide in overcoming lettuce seed thermodormancy. Plant Physiol 51: 1089–1094

20. REYNOLDS T 1973 A temperature-dependent source of variability in estimates of germination behavior of lettuce fruits. Planta 113: 327–332
21. REYNOLDS T 1975 Characterization of osmotic restraints on lettuce fruit germination. Ann Bot 39: 791–796
22. REYNOLDS T 1975 pH restraints on lettuce fruit germination. Ann Bot 39: 797–805
23. REYNOLDS T, PA THOMPSON 1971 Characterization of the high temperature inhibition of germination of lettuce. Physiol Plant 24: 544–547
24. REYNOLDS T, PA THOMPSON 1973 Effects of kinetin, gibberellin and (±) abscisic acid on the germination of lettuce (*Lactuca sativa*). Physiol Plant 28: 516–522
25. SCHEIBE J, A LANG 1969 Lettuce seed germination effects of high temperature and of repeated far red treatment in relation to phytochrome. Photochem Photobiol 9: 143–150
26. SMITH H 1975 Phytochrome and Photomorphogenesis. McGraw-Hill, London
27. SPEER HL, D TUPPER 1975 The effect of lettuce seed extracts on lettuce seed germination. Can J Bot 53: 593–599
28. SPEER HL, AI HSIAO, W VIDAVER 1974 Effects of germination promoting substances given in conjunction with red light on the phytochrome mediated germination of dormant lettuce seeds. Plant Physiol 54: 852–854
29. TAKEBA G, S MATSUBARA 1976 Analysis of temperature effect on the germination of New York lettuce seeds. Plant Cell Physiol 17: 91–101
30. TAYLORSON RB, SB HENDRICKS 1973 Phytochrome transformation and action in seeds of *Rumex crispus* L. during secondary dormancy. Plant Physiol 52: 475–479
31. THOMPSON PA 1970 The characterization of the germination response to temperature of species and ecotypes. Nature 255: 827–831
32. THOMPSON PA, SA COX, RH SANDERSON 1979 Characterization of the germination response to temperature of lettuce (*Lactuca sativa* L.) achenes. Ann Bot 43: 319–334
33. TOOLE VK 1973 Effects of light, temperature and their interactions on the germination of seeds. Seed Sci Technol 1: 339–396
34. VIDAVER W, AI HSIAO 1974 Actions of gibberellic acid and phytochrome on the germination of Grand Rapids lettuce seeds. Plant Physiol 53: 266–268
35. VIDAVER W, AI HSIAO 1975 Secondary dormancy in light-sensitive seeds incubated anaerobically or at elevated temperature. Can J Bot 22: 2557–2560