HORTSCIENCE 28(8):786-788. 1993.

The Role of Light during *Phlox drummondii* Hook. Seed Germination

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Additional index words. irradiance intensity, irradiance duration

Abstract. **The role of light on phlox germination and radicle emergence was studied. Neither light level nor duration affected total germination (G) percentages, which ranged from 93%. to 98%. Increasing light level and lengthening light duration delayed achieving 50% of final germination (T_{50}) and increased the span in days between 10% and 90% germination (T_{90} - T_{10}). Increasing light duration from 0 to 24 hours during germination at 0.15 µmol·s^{-1}·m^{-2} progressively increased T_{50} from 3.5 to 7.1 days and T_{90} - T_{10} from 2.6 to 13.1 days. Similarly, lengthening light duration from 0 to 24 hours at 1.5 µmol·s^{-1}·m^{-2} light increased T_{50} from 3.7 to 10.8 days and T_{90} - T_{10} from 2.8 to 13.4 days, whereas 15 µmol·s^{-1}·m^{-2} increased T_{50} from 3.9 to 21.9 days and T_{90} - T_{10} from 2.9 to 29.2 days. Increasing the number of days in darkness from 0 to 6 decreased T_{50} from 14.8 to 4.3 days and T_{90} - T_{10} from 20.2 to 3.5 days. Increasing the number of days in light from O to 6 increased T_{50} from 4.0 to 8.9 days and T_{90} - T_{10} from 3.8 to 8.2 days. Estimated rates of decline or increase in T_{50} and T_{90} - T_{10} with each added day in darkness or light were measured by fitting regression equations. Seeds germinated in continuous darkness or in 24 or 48 hours of light followed by total darkness had similar G, T_{50}, and T_{90} - T_{10}. The results indicate that initial phlox seed germination was not affected by light, but that light inhibited radicle extension in later germination stages.**

Light is one of several environmental factors that influence seed germination rate. Light has been recognized since the mid- 19th century as a germination-controlling factor (Crocker, 1930). More recent research has demonstrated that light acts in dormancy induction or release and often interacts with temperature (Toole, 1973). Hartmann et al. (1990) reported that the seeds of most light-sensitive species had physiological dormancy; some needed light and others needed darkness or far-red light for germination. The short-term exposure of imbibed seeds to white light for seconds or minutes neither inhibits nor promotes germination; to affect germination, irradiation or darkness is needed for many hours (Bewley and Black, 1982). Khan (1977) found that light sensitivity of individual members in a seed population may vary widely. The germination of some seeds in each lot was inhibited by just a few hours of light, whereas that of others was prevented only by light for many hours or continuously.

The basic mechanism of light sensitivity in seeds involves phytochrome, a photochemically reactive pigment found in the seeds of all species (Bewley and Black, 1985; Taylorson and Hendricks, 1977). Exposing imbibed seeds to white or red light causes the red phytochrome to change to the far-red phytochrome, which stimulates germination of light-requiring seeds. Exposing seeds to far-red light or prolonged periods of darkness causes a change to red phytochrome, which promotes germination in darkness-requiring seeds. Bewley and Black (1985) reported that the initial dormancy of light-requiring seeds was broken under long-term illumination with white light. However, radicle extension was inhibited in later germination stages by the same light duration. It was not determined if phytochrome inhibited radicle extension.

Hartmann et al. (1990) list phlox in a small group of species in which germination is prevented by light, and Cathey (1976) recommended continuous darkness during phlox seed germination. Carpenter et al. (1993) reported that phlox seed germinated in darkness had similar total germination (G) percentages over a wide range of constant or alternating temperatures, but germination occurred earlier and was more uniform at constant 20 or 25C and alternating 20/25C than lower or higher temperatures. Our research objectives were to determine if light causes reduced and irregular phlox seed germination by inducing seed dormancy or inhibiting or delaying radicle extension.

Seed light and germination procedures. 'Light Salmon' phlox seeds were received from Sluis and Groot Quality Seeds, Enkhuizen, Holland, in Nov. 1991, 5 weeks after harvest. Seeds were dusted with 3α,4,7,7α-tetrahy dro-2[(trichloromethyl) thio]-1*H*-isolindole-1,*3(2H)*-dione (captan) in all studies. Treatments contained four 100-seed replications, which were germinated in individual 9-cm petri dishes on blue blotter paper 100 (Anchor Paper Co., Charlotte, N. C.) saturated with 6 ml of distilled water. Seeds were germinated in incubators (model 17-5RG, Stults Scientific Engineering Corp., Springfield, Ill.) equipped with timers to control light duration and incandescent dimmers (Lutron Co., Coopersburg, Pa.) to establish light level from 60-W incandescent lamps. Petri dishes were placed on a shelf 3 cm above the incubator floor before establishing 0.15, 1.5, or 15 µmol·s^{-1}·m^{-2} light levels using a quantum-radiometer photometer, (model 185A; LI-COR, Lincoln, Neb.). Petri dishes were rotated within and among chambers daily during light periods, although light levels among locations within incubators never exceeded ± 4% from the established level,

In each study, germinated seeds were counted daily; seeds with radicle protrusion through the testa were considered germinated. Seeds germinated in darkness were counted in dim light (0.21 µmol·s^{-1}·m^{-2} of photosynthetically active radiation) from a 25-W green lamp. G, days to 50% of final germination (T_{50}), and germination span in number of days between 10% and 90% germination (T_{90}– T_{10}) were calculated from the data as described by Furutani et al. (1985).

In each study, the data were subjected initially to analysis of variance to determine if the treatments-specific days of receiving 24 h of light, number of days in darkness or in light, and different light levels-differed. When a significant ($P \leq 0.05$) difference among treatments was found, trends in the average G, T_{50}, and T_{90}-T_{10}, over days of darkness or days of light, were measured by fitting linear and quadratic regression equations. In the case of a linear trend, e.g., T_{50} over days of darkness, the simple regression equation is $T_{50} = b_o + b_1 \times$ dark days and the slope or rate of change in the estimated T_{50} values per a 1 -day increase in darkness is constant and denoted by b,. When the trend is quadratic, the quadratic regression equation is $T_{50} = b_o + b_1 \times$ dark days + $b_2 \times$ dark days' and the slope is not constant, but changes with each day of darkness. With the quadratic equation, the slope is calculated as $b_1 + 2b_2 \times$ dark days. Once a fitted regression equation was selected, the percent of the total variation explained by the equation is given by R^2.

Changes in germination from 24 h of light. Seeds were germinated in darkness at 20C, except for one 24-h period of light at 15 µmol·s^{-1}·m^{-2} light during day 1,2,2.5,3,4,5, or 6. Other treatments received continuous light or darkness during 28 days of the study. 'Light Salmon' was selected for this and subsequent studies because of high G and short T_{50} and T_{90}– T_{10} when germinated in darkness (data not presented). Differences among treatmentsweretested for G, T_{50}, and T_{90}– T_{10} using analysis of variance and, for specific comparisons, protected least significant difference.

Determining the effect of light or darkness during germination. In the first study, seeds received 1, 2, 3, 4, 5, or 6 days of darkness during germination, followed by continuous light at 15 µmol·s^{-1}·m^{-2}. Another seed treatment was continuous light for 28 days. In the

Receivedfor publication 6 Nov. 1992. Accepted for publication 11 Mar. 1993. Florida Agriculture Experiment Station Journal series no. R-02772. We acknowledge the seed source as Sluis and Groot Quality Seeds, Enkhuizen, Holland. This research wassponsoredpartiallyby a grant from the Bedding PlantsFoundation, Lansing, Mich. The cost of publishing this paper was defrayed in part by the paymentofpagecharges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.
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second study, seeds received progressively more days of light during germination, with 1, 2, 3, 4, 5, or 6 days of light followed by darkness. This study also included seeds that received continuous darkness for 28 days. Seeds with emerged radicles were counted daily, and trends in G, T_{50}, and T_{90}- T_{10}, when taken over the number of days in light or dark, were modeled by fitting regression equations.

Effect of light level and daily duration on germination. Seeds were irradiated with 0.15, 1.5, or 15 µmol·s^{-1}·m^{-2} of white light from incandescent lamps for 0, 1,6, 12, 18, or 24 h daily and germinated at 20C for 42 days. Air temperatures in incubators were reduced to 18C during light periods at 15 µmol·s^{-1}·m^{-2} to maintain 20C in petri dishes. In preliminary studies, thermocouples placed on the blotter paper in petri dishes measured temperatures that were recorded at 6-h intervals by a recording potentiometer (Easterline Angus Instrument, Indianapolis). Adequate moisture content of the blotter paper was maintained by adding sufficient distilled water daily to saturation. The effects of light level, light duration, and the light level x duration interaction were investigated in the analysis of variance.

One 24-h light (15 µmol·s^{-1}·m^{-2}) period interrupting darkness at various germination stages had no effect on 'Light Salmon' G. Average G ranged from 93%, when seeds were lighted on day 1, to 96%, when seeds were lighted on day 6. Seeds exposed either to continuous light or continuous darkness averaged 94% G. The only significant $(P \leq 0.01)$ differences found in days to T_{50} and $T_{90}- T_{10}$ were with seeds receiving continuous light having higher T_{50} (14.6 days) and $T_{90}- T_{10}$ (21.0 days) than the T_{50} (4.0 to 5.2 days) and $T_{90}- T_{10}$ (3.8 to 5.1 days) for seeds germinated in continuous darkness or those receiving one to six 24-h light periods (data not presented).

Average G for seeds germinated in continuous light, continuous darkness, or varying combinations of light and darkness during germination were similar (Tables 1 and 2). Average T_{50} differed significantly $(P \leq 0.01)$ when the number of days in darkness (Table 1) or light increased during germination (Table 2). As the number of days in darkness increased from 0 (continuous light) to 6, the average number of days to achieve T_{50} progressively declined (Table 1, Fig. 1). The quadratic regression equation expressing T_{50} as a function of the number of dark days is $T_{50} = 15.4 - 4.3 \times$ dark days + 0.42 × dark days^2, $R^2 = 0.93$. The slope or rate of decrease in T_{50} for each day in darkness is estimated from the equation slope = (-4.3) + 0.8 × dark days. At 1,2,3, or 4 days of darkness, for example, the estimated decreases in T_{50} are 3.5,2.7, 1.9, and 1.1 days, respectively.

Predicting T_{50} for seeds in darkness for any period ranging from 0 to 6 days is possible by using the equation above. Also, to estimate the average number of dark days, seeds must be kept in darkness to achieve some value of T_{50}, e.g., $T°_{50}$. This latter number of days is calculated by solving for the roots, d, of the equation $0= (15.4 - T°_{50})-4.3 x d+0.4 x d^2$. For example, for seeds to achieve T_{50} by $T°_{50} = 7.7$ days,

Table 1. Total germination rate (G), 50% germination (T_{50}) and span ($T_{90}-T_{10}$) of 'Light Salmon' phlox under various numbers of days in darkness before continuous light[z]. Data are means of four 100-seed replications during 28 days of germination.

Darkness duration (days)	G (%)	T_{50} (days)	$T_{90}-T_{10}$ (days)
0	90	14.8	20.2
1	90	12.7	17.4
2	92	8.1	14.5
3	89	5.7	8.1
4	91	4.6	5.3
5	92	4.5	4.2
6	93	4.3	3.5
Linear	NS	*	*
Quadratic	NS	*	*
R^2	NS	0.93	0.88

[z]Light intensity was 15 µmol·s^{-1}·m^{-2}.
[NS,*]Nonsignificant or significant at $P \leq 0.01$, respectively.

Table 2. Total germination rate (G), 50% germination (T_{50}), and span ($T_{90}-T_{10}$) of 'Light Salmon' phlox under various numbers of days in light[z] before darkness. Data are means of four 100-seed replications during 28 days of germination.

Light duration (days)	G (%)	T_{50} (days)	$T_{90}-T_{10}$ (days)
0	94	4.0	3.8
1	93	4.3	3.8
2	95	4.7	3.7
3	92	5.9	5.1
4	96	6.7	6.1
5	93	7.5	6.7
6	94	8.9	8.2
Linear	NS	**	**
Quadratic	NS	**	*
R^2		0.91	0.70

[z]Light intensity was 15 µmol·s^{-1}·m^{-2}.
[NS,*,**] Nonsignificant or significant at $P \leq 0.05$ or 0.01,

which is one-half the time estimated by the equation above for seeds in continuous light to reach $T_{50} = 15.4$, at least d = 2.3 days of darkness are required. The d = 2.3 value is shown in Fig. 1 as the number of dark days corresponding to 7.7 on the T_{50} curve.

As with T_{50}, $T_{90}- T_{10}$ decreased quadratically as the number of days in darkness increased from 0 to 6 (Table 1, Fig. 1). The fitted quadratic regression equation relating T_{90}–T_{10} to days in darkness is T_{90}: $T_{10} = 21.2 - 4.9\times$ dark days + 0.3 × dark days^2, $R^2 = 0.88$. The estimated rate of decrease in $T_{90}- T_{10}$ for each day in darkness is slope = (-4.9) + 0.6 × dark days. Seeds receiving 2.6 days or more of darkness are estimated to have a span of at most 10.6 days, which is one-half the estimated span of seeds receiving continuous light.

As the number of days in light during germination increased from O to 6, the days to T_{50} increased quadratically (Table 2, Fig. 2). This increase is expressed by the regression equation $T_{50} = 3.9 + 0.3\times$ light days + 0.08 × light days^2, $R^2 = 0.93$. The rate of increase in T_{50} for each day in light is expressed as slope =0.3 +0.2× light days. Similarly, the days for $T_{90}- T_{10}$ also increased quadratically when seeds received more days of light. The fitted

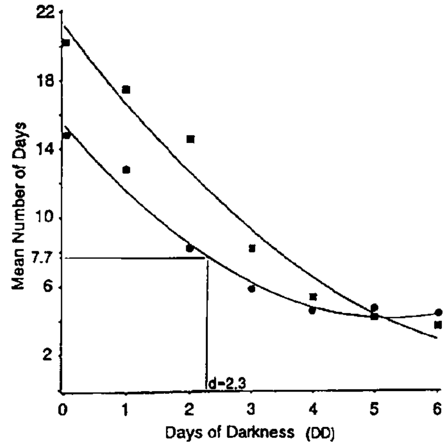


Fig. 1. Effect of number of days of darkness on mean days to 50% germination (T_{50}) (●) and span between 10% and 90% germination ($T_{90} - T_{10}$) (■) of 'Light Salmon' phlox seeds.

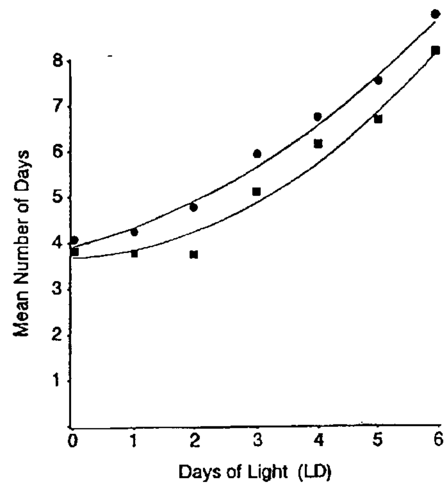


Fig. 2. Effect of number of days of light on mean days to 50% germination (T_{50}) (●) and span between 10% and 90% germination ($T_{90}- T_{10}$) (■) of 'Light Salmon' phlox seeds.

regression equation for $T_{90}- T_{10}$ was T_{90}- T_{10} = 3.7+ 0.4 × dark days + 0.12 × dark days^2, R^2 = 0.75, with a corresponding slope formula of slope = 0.4 + 0.24 × dark days.

Neither light level (0.15, 1.5, or 15 µmol·s^{-1}·m^{-2}) nor light duration (0, 1,6, 12, 18, or 24 h) affected G, with G ranging between 92% and 98%, for all combinations of level and duration (data not presented). Both light level and duration affected the number of days to T_{50}. Also, a significant $(P < 0.01)$ interaction was found between light level and duration on T_{50}. Lengthening daily light received during germination increased T_{50} at each light level, with the effect of duration increasing with increased light (Fig. 3). Light level had little effect on T_{50} at daily durations below 6 h; but, at 12-h durations and above, T_{50} increased curvilinearly, with the degree of curvilinearity increasing with light level. Thus; the higher the level of light the greater the curvilinear increase in T_{50} with increased light duration.

Light level and duration affected $T_{90}- T_{10}$, and a significant $(P \leq 0.01)$ interaction was

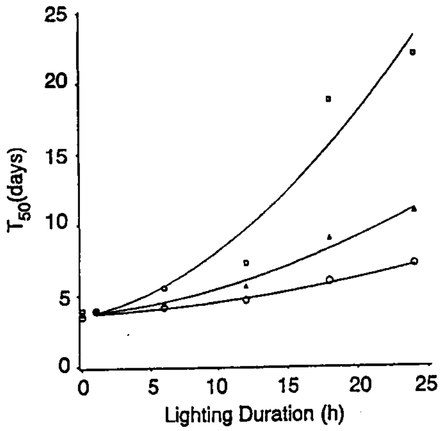
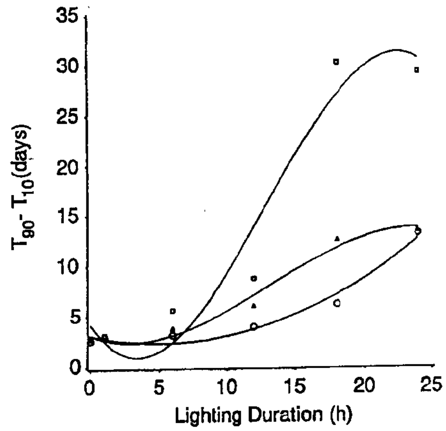


Fig. 3. Days to 50% germination (T_{50}) for 'Light Salmon' phlox germinated at 0.15 (❍), 1.5 (▲), or 15 $\mu mol \cdot s^{-1} \cdot m^{-2}$ (❑) light levels and 0-,6-, 12-, 18-, or 24-h durations. The quadratic equations relating T_{50} to light duration at each light level areas follows: 0.15 $\mu mol \cdot s^{-1} \cdot m^{-2}$, $T_{50} = 3.65 + 0.04d + 0.0042d^2$, $R^2 = 0.91$; 1.5 $\mu mol \cdot s^{-1} \cdot m^{-2}$, $T_{50} = 3.68 + 0.08d + 0.0094d^2$, $R^2 = 0.97$; and 15 $\mu mol \cdot s^{-1} \cdot m^{-2}$, $T_{50} = 3.55 + 0.19d + 0.0262d^2$, $R^2 = 0.93$.



Fig, 4. Span between 10% and 90% germination ($T_{90} - T_{10}$) in days for 'Light Salmon' phlox germinated at 0.15 (m), 1.5 (s), or 15 $\mu mol \cdot s^{-1} \cdot m^{-2}$ (q) light levels and 0-,6-,12-,18-, or 24-h durations. The equations illustrating the effect of light duration on $T_{90} - T_{10}$ were cubic at 1.5 and 15 $\mu mol \cdot s^{-1} \cdot m^{-2}$: 0.15 $\mu mol \cdot s^{-1} \cdot m^{-2}$, $T_{90} - T_{10} = 3.06 + 0.29d + 0.029d^2$, $R^2 = 0.95$; 1.5 $\mu mol \cdot s^{-1} \cdot m^{-2}$, $T_{90} - T_{10} = 3.05 + 0.51d + 0.101d^2 - 0.003d^3$, $R^2 = 0.97$; 15 $\mu mol \cdot s^{-1} \cdot m^{-2}$, $T_{90} - T_{10} = 4.18 + 2.02d + 0.341d^2 - 0.009d^3$; $R^2 = 0.93$.

detected (Fig. 4). At 0 and 1 h, $T_{90} - T_{10}$ values at the three light levels were similar. At ≤ 6 h of light, $T_{90} - T_{10}$ increased as light levels increased, except at 24 h, where $T_{90} - T_{10}$ values at 0.15 and 1.5 $\mu mol \cdot s^{-1} \cdot m^{-2}$ were similar. At both 1.5 and 15 $\mu mol \cdot s^{-1} \cdot m^{-2}$, maximum or near maximum $T_{90} - T_{10}$ occurred after 18 h of light. The cubic trends in $T_{90} - T_{10}$ (Fig. 4) at the 1.5 and 15 $\mu mol \cdot s^{-1} \cdot m^{-2}$ light levels are the result of the large increase in $T_{90} - T_{10}$ between 12 and 18 h of light followed by the small change in $T_{90} - T_{10}$ from 18 to 24 h.

Commercial recommendations for germinating phlox include covering seeds with a layer of medium (Ball, 1985), and Hartmann et al. (1990) reported that the seeds required darkness for germination. Our results showed that G was similar for seeds germinated in either continuous light or darkness, but germination in continuous darkness was more rapid and uniform. No differences were found in G, T_{50}, or $T_{90} - T_{10}$ of seeds germinated in continuous darkness or light for the first 24 or 48 h after sowing before being placed in continuous darkness. Bewley and Black (1982) reported that light is required for lettuce *(Lactuca sativa* L.) germination shortly after seed imbibition. Our results showed that phlox seed germinated well in both light or darkness, in contrast to the previous report of Hartmann et al. (1990), thus suggesting that germination was independent of phytochrome.

Bewley and Black (1985) reported that light can modify seed germination at two periods during germination. Exposing 'Grand Rapid's' lettuce seed to red or white light immediately after imbibition removed seed dormancy and promoted germination, but light received 4 to 8 h after the promotive exposure inhibited or delayed germination. Karssen (1981) reported that lambsquarter *(Chenopodium albium* L.) seed receiving light during root elongation in germination stage 3 had delayed germination and reduced radicle elongation. Bewley and Black (1982) reported that light delays seed germination by stopping or reducing radicle cell elongation. Our results suggest the radicle–hypocotyl axis could be the point of retardation, since radicle and plumule emergence was delayed by light (data not presented). Lighting phlox seed the first 48 h after sowing had little or no effect on T_{50} or $T_{90} - T_{10}$, but both intervals increased for each 24 h of light above 48 h when evaluated from 0 to 6 days. This result indicates that seeds must receive light at just the right time for germination to be arrested.

The period of light causing the greatest delay in T_{50} and $T_{90} - T_{10}$ for phlox was approximated by reducing the number of days in darkness from 6 to 1. Seeds germinated in darkness had T_{50} and $T_{90} - T_{10}$ values of 4.0 and 3.8 days, respectively. Transferring seeds to continuous light after ≤ 3 days in darkness delayed germination, giving an estimated T_{50} of ≤ 6.2 days and a $T_{90} - T_{10}$ of ≤ 9.4 days (Fig. 1).

Commercial bedding plant producers know that phlox seeds require darkness during germination, and direct sowing in plug trays and germination in the greenhouse require covering seeds with a fine layer of medium. They believe that light at low levels has little or no effect on phlox germination since most seeds germinate. Our results showed that no difference in G occurred among treatments receiving 0.15, 1.5, 15 $\mu mol \cdot s^{-1} \cdot m^{-2}$, or darkness (data not presented), but T_{50} and $T_{90} - T_{10}$ increased with light duration and level. The curvilinear trend for T_{50} (Fig. 3) suggested that longer delays could result at higher light levels than those used in this study. Similarly, the maximum values of $T_{90} - T_{10}$ at 18- and 24-h light durations and 15 and 1.5 $\mu mol \cdot s^{-1} \cdot m^{-2}$ light levels, respectively, suggested that the maximum $T_{90} - T_{10}$ may have been attained at these levels. We found no research that studied the effect of light level on T_{50} or $T_{90} - T_{10}$. Karssen (1981) used one level (43 $\mu mol \cdot s^{-1} \cdot m^{-2}$) of light in studies that determined that light reduced radicle elongation. The progressive lengthening of T_{50} and $T_{90} - T_{10}$ as light levels and duration increased indicated that the response was not caused by photoperiod.

These studies help us understand the frequent reports of slow and irregular phlox seed germination. The data presented show that G was independent of darkness-similar in light or darkness. However, light influenced the time required for germination, even at low (0. 15 and 1.5 $\mu mol \cdot s^{-1} \cdot m^{-2}$) light levels and short durations (one 24-h period at 15 $\mu mol \cdot s^{-1} \cdot m^{-2}$). Supplemental or incidental light that could extend normal daylengths to 18 or 24 h in greenhouses caused greater germination delays and more irregular germination than shorter light periods. Light was found to cause slower and more irregular germination by delaying root emergence during the last germination stage, thus increasing T_{50} and $T_{90} - T_{10}$. This information should help develop recommendations for improved phlox seed germination and alert commercial growers that delayed or irregular germination can be caused by light.

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