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Watermelon seed germination. 1. Effects of light, temperature and osmotica

C. A. Thanos* and K. Mitrakos

Institute of General Botany, University of Athens, 15784 Athens, Greece

Abstract

Seeds of watermelon (*Citrullus lanatus* cv. Sugar Baby) germinated optimally in the dark, throughout the range 20–40°C. Germination was inhibited by continuous (c) irradiation with far-red (FR), blue or white incandescent light; short pulses were ineffective. Intermittent FR could fully substitute for cFR; the effect of alternating red and FR pulses during 30-min dark cycles depended upon the timing of the illuminations within each cycle. It is concluded that germination in watermelon is controlled by the low-energy reaction of phytochrome. However, continuous and intermittent red light resulted in partial reductions in germinability. Opening the seed coat at the radicle end enhanced germination in the dark and reduced photosensitivity towards FR. The outer, lignified part of the testa exerted a mechanically restrictive force upon the expanding radicle; this force was estimated to be equivalent to 0.3 MPa. The kinetics, at 25°C in the dark, of the time course of germination and the escape from the inhibitory actions of cFR and osmoticum (0.5M mannitol) were all sigmoid curves, which, upon transformation to normal distributions, had different means, but statistically similar variances. The cFR-irreversible activation of germination by phytochrome and the mannitol-irreversible onset of radicle elongation preceded radicle protrusion (mean at 32 h, 25°C) by 8 and 6 h, respectively. From the results and data on imbition, it is concluded that activation of germination in watermelon takes place during the second, stationary phase of imbibition (20–30 h after sowing at 25°C).

Keywords: *Citrullus lanatus*, osmotic inhibition, photoinhibition, phytochrome, seed coat, germination, watermelon

* Correspondence

Introduction

Seeds of the family Cucurbitaceae have been reported to germinate in the dark. In a pioneering study, Nakamura *et al.* (1955) found that germination of *Citrullus lanatus*, *Cucurbita maxima*, *Lagenaria siceraria*, *Benincasa hispida* and *Momordica harantia* was hindered by continuous white light throughout the temperature range tested (20–30°C), while germination of *Cucumis sativus*, *C. melo* and *C. melo* var. *conomon* was inhibited only at 20°C. The light source used consisted of fluorescent tubes; a wavelength-dependence experiment revealed inhibitory action by the blue and far-red regions (but not by the green one). In subsequent investigations, light inhibition by prolonged white, far-red or blue illumination was reported for seeds of *Citrullus colocynthis* (Koller *et al.*, 1963), *Cucumis sativus* (McDonough, 1967; Yaniv *et al.*, 1967), *C. anguria* (Noronha *et al.*, 1978) and *Citrullus lanatus* (cv. Sugar Baby: Sachs, 1977; Thanos, 1984; dwarf WB-2: Loy and Evensen, 1979; wild-grown: Botha *et al.*, 1982a,b).

In the present work, seeds of Sugar Baby watermelon were used in a study of the effects of temperature, seed coat and light, and their interactions, in the overall control of germination. As information on the seed physiology of wild-grown watermelon has been reported (Botha *et al.*, 1982a,b, 1984; Botha and Small, 1988), the germination of a watermelon cultivar was compared with that of its wild-grown ancestor.

Materials and methods

Plant material

Seeds of the watermelon (*Citrullus lanatus* [Thunb.] Matsu. et Nakai,) cultiver Sugar Baby were purchased from KYDEP, Greece, The mean seed weight was 43.1 ± 1.1 mg, mean testa weight 20.3 ± 0.5 mg and seed moisture content 7.0% (on a fresh weight basis). Seed batches were stored in moisture- and light-proof containers at room temperature (20 ± 5°C). Throughout the experiment, no

changes in germination characteristics were observed. Testa removal and 'opening' of seeds were performed manually. The former procedure did not include the removal of the transparent, membranous, inner layer that is 2–3 cells thick (chlorenchyma in other Cucurbitaceae, according to Bhatnagar and Johri, 1972; perisperm plus endosperm according to Botha *et al.*, 1982a and Welbaum and Bradford, 1990). Seeds were 'opened' by applying lateral pressure, which resulted in cracking across the suture of the seed coat, at the radicle end. Observations of testa structure under a stereomicroscope revealed differentiation into five zones, a characteristic of the cucurbitaceous seed coat (Bhatnagar and Johri, 1972). Dramatic anticlinal elongation of the cells of the seed epidermis was evident upon moistening, resulting in more than tripling of the initial thickness in about 30 s. Meanwhile, a thin mucilage layer appeared on the seed coat surface. This constitutes the well-known phenomenon of myxospermy (van der Pijl, 1972), though it has not been reported for cultivated (e.g. Loy and Evensen, 1979) or wild-grown (e.g. Botha *et al.*, 1982a,b) watermelon.

Germination conditions

Imbibition and germination tests were carried out with at least eight samples of 25 seeds sown in glass Petri dishes, 9 cm in diameter, lined with two filter paper discs moistened with 6 ml of deionized water or mannitol solution. The tests were performed in plant growth chambers (Enviratrol, model EY8VH, Conviron, Canada) and the temperature was kept constant within ± 0.5°C of the value set. The criterion of germination was visible protrusion of the radicle (by approx. 0.3 mm), and germinated seeds were discarded. Each value presented in this study was derived from an independent sample (except for the time course in Fig. 8); vertical bars and $\pm$ values represent standard error (SE).

Light sources

The various broad-band irradiations were produced by a bank of bulbs or tubes and the light was filtered through an appropriate combination of coloured Plexiglas sheets (each 3 mm thick, Röhm GmbH, Germany). White (fluorescent) light (total flux density 32.2 μmol m^{-2} s^{-1}) was obtained from six cool-white fluorescent tubes (F 48T12.CW.1500, General Electric); white (incandescent) light (10.5 μmol m^{-2} s^{-1}) was from four tungsten-filament bulbs, 40 W each (Osram); blue (B) light (1.9 μmol m^{-2} s^{-1}) was produced by eight blue fluorescent tubes (TL 20W/18, Philips) and one layer of blue Plexiglas, 627; red (R) light (11.0 μmol m^{-2} s^{-1}) was produced by eight red fluorescent tubes (TL 20W/15, Philips) and one layer of red Plexiglas, 501; and far-red, (FR) light (18.2 μmol m^{-2} s^{-1}) was obtained by 12 incandescent tubes (Philinea 6276X60 W, Philips) and filtered through three layers of Plexiglas (two blue, 627, and one red, 501), and a water bath 10 cm deep.

Monochromatic irradiations were obtained with interference filters (Schott, Germany) placed in a special frame along the light path of a slide projector. The photon flux densities for 442, 482, 639 and 662 nm were, respectively, 6.3, 6.9, 12.8 and 13.3 μmol m^{-2} s^{-1}.

All manipulations of seeds that had imbibed were carried out under a dim green safelight (0.05 μmol m^{-2} s^{-1}; one green fluorescent tube F 15T8.G.6, 15 W Green-Photo, General Electric, USA, two Plexiglas sheets, one red-orange, 478, and one green, 700). Total flux density values refer to light in the visible range (400–800 nm) at the seed surface, estimated from the measurements taken with a spectroradiometer (ISCO SR, USA).

Results

Nearly 100% germination was obtained in darkness and under red or white (fluorescent) light (Table 1). Inhibition of germination was greater under far-red light than under white (incandescent) or blue light. With decreasing flux densities of continuous far-red (cFR), significant germination percentages were obtained; this enhancement was particularly marked in opened seeds (Table 2). The photosensitive site of germination was in the radicle half of the seed; in seeds half-immersed in black (inked) agar and under cFR, germination occurred only when the cotyledon end was exposed.

The course of germination in the dark at 25°C (Fig. 1) followed a typical sigmoid curve, with a 7-h lag phase after the initial manifestation of germination (at 20 h) in a small fraction of the seed population. Nearly 90% of the seeds germinated between 27 and 37 h after the onset of imbibition; T_{50} (time needed for 50% germination) was estimated

Table 1. Effect of light on germination of watermelon seed at 25°C

Light treatment	Germination (% ± SE)
Darkness	97.5 ± 1.1
White: fluorescent	96.0 ± 1.1
incandescent	25.5 ± 2.4
fluorescent + incandescent	88.5 ± 1.2
Red	97.0 ± 1.0
Far-red	0.0 ± 0.0
Blue	35.0 ± 3.2

Light treatments were given continuously from the onset of imbibition until the final germination percentage was scored. Flux densities as quoted under Light sources.

Table 2. Germination of watermelon seeds, at 25°C, as a function of flux density of continuous, broad-band, far-red irradiation

Far red Flux density (μmol m^{-2} s^{-1})	Germination (% ± SE)	
	Intact seeds	Opened seeds
5.0	0.0±0.0	0.0±0.0
1.6	1.8±0.8	0.0±0.0
0.8	12.5±1.8	11.0±1.8
0.6	15.5±2.1	23.0±2.7
0.5	31.8±2.1	47.8±3.0
0.3	36.0±2.8	83.0±2.4

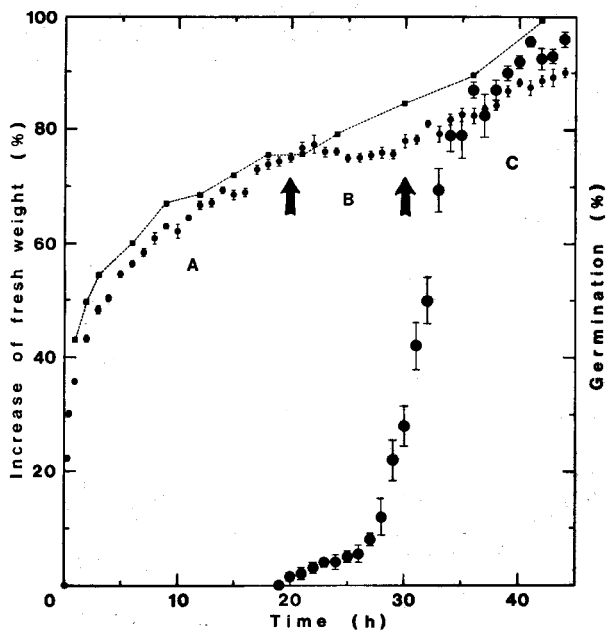

Figure 1. Time courses of germination (●) of watermelon seed and water uptake ((•) intact seeds, (▪) opened seeds), at 25°C in darkness. The arrows indicate the boundaries between consecutive phases of water uptake, for intact seeds. Vertical bars represent 2 SE. The third phase of water uptake in intact and opened seeds follows linear regression curves, given respectively by the equations

$Y = 77.252 + 0.983\ X$ ($r^2 = 0.960$, d.f. = 118, $P < < 0.001$)

and

$Y = 75.494 + 1.054\ X$ ($r^2 = 0.981$, d.f. = 38, $P < < 0.001$);

X being time (h) set to 0 at hours 30 and 21, respectively, and Y fresh weight increase (% of the initial 'dry' seed weight).

as 32.2 h and germination was completed well before 48 h.

Water uptake for intact seeds in darkness, at 25°C, showed three distinct phases (Fig. 1). Phase A (passive absorption of water) lasted for 20 h and seemed to follow exponential kinetics (of the form $I = I_{final}$ $(1 - e^{-kt})$. Nevertheless, in an additional study of imbibition (data not shown), isolated seed coats increased rapidly in fresh weight (90% after 1 h, reaching a maximum increase of 116% after 6 h); on the other hand, isolated embryos imbibed much more slowly and considerably less (maximum increase 51%). Phase B (stationary phase) lasted for approx. 10 h (20–30 h after the onset of imbibition), and throughout this period fresh weight was maintained at a constant 76% above the initial seed weight. Phase C (active uptake of water) started at hour 30 and the kinetics of fresh weight increase followed a linear regression curve. On the other hand, seeds imbibing under cFR (and therefore fully inhibited from germinating, see Table 1) followed identical kinetics (data not shown) during phases A and B, but phase C did not occur. From hour 20, seed fresh weight was constant at around 80%.

Water uptake for opened seeds followed, in comparison with that of intact seeds, a faster (by 2–3 h) initial increase (phase A); as a consequence, phase B was reached after approx. 17 h. The stationary phase was considerably shorter than in intact seeds (only 4 h, from hour 17 to hour 21); the third phase followed a linear regression curve, parallel to that of intact seeds.

Dark germination as a function of temperature (Fig. 2) was nearly 100% at 20–40°C; it decreased sharply at 15 and 42.5°C. Under cFR (of the same flux density as in Table 1), germination was partially

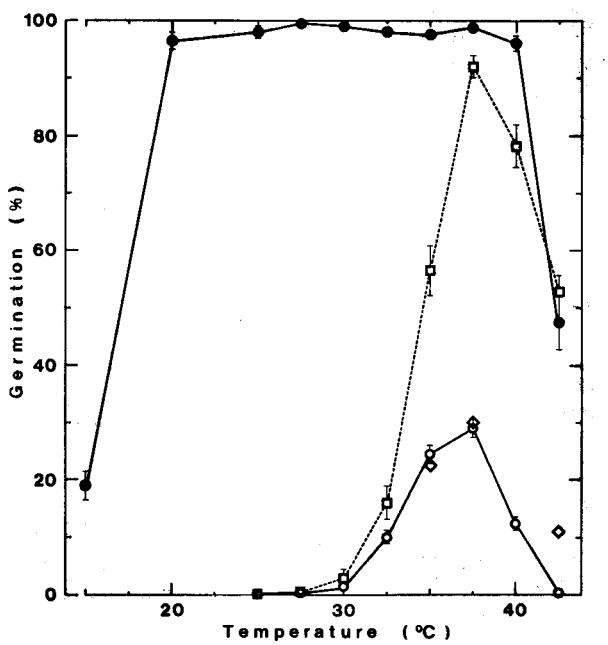

Figure 2. Final germination percentage of watermelon seeds as a function of temperature, in darkness (●) or under continuous far-red light (in intact seeds (○); and in opened seeds imbibed in water (□) or 0.1M mannitol (◇). Vertical bars represent 2 SE.

manifested at 30–40°C, with a maximum value of approx. 30% at 37.5°C, but, in opened seeds, germination was considerably enhanced (a maximum of >90% at 37.5°C, while the range was not affected). Moreover, when opened seeds were soaked in 0.1M mannitol solution, instead of water, the germination percentages were identical to those for intact seeds.

The enhancement of germination in opened seeds by high temperature was further investigated (Fig. 3): 37.5°C allowed full promotion if applied at the second 12 h period after the onset of imbibition. Earlier and later applications were less effective. Less than 12 h of high-temperature treatment was unsuccessful (data not shown). Thus, 10, 8 and 6 h at 37.5°C, timed in several ways within 12 and 24 h after the onset of imbibition, resulted in no more than 83, 76.5 and 27.5% germination, respectively.

Upon imbibition by seeds in mannitol solutions (at 25°C, in the dark), a germinability gradually decreased as a result of the increasing osmotic concentration (Fig. 4). The resulting 'germination potential curves' in all three seed 'types' followed similar sigmoid kinetics. Germination of opened and decoated seeds did not differ significantly; full inhibition required 0.6M, while for intact seeds 0.4M sufficed. Half-inhibition of germination was obtained with approx. 0.42 and 0.30M, respectively. These values correspond to osmotic potentials (Ψ_s) of -1.04 and -0.74 MPa; the shift between the curve of intact seeds and that of opened and decoated seeds is 0.12M or 0.30 MPa.

The kinetics of escape from the inhibitory actions of either cFR or a concentrated (0.5M) mannitol solution are shown in Fig. 5. When seeds imbibed in darkness in water for various periods were then transferred to cFR, the resulting germinability curve was a typical sigmoid one, similar in shape to the

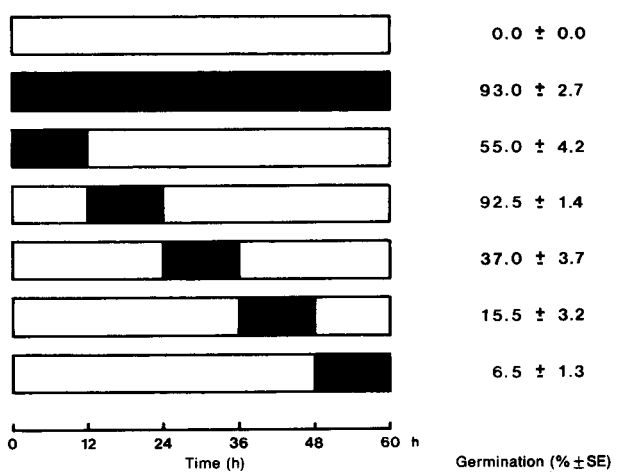

Figure 3. Effect of high temperature on the germination of opened watermelon seeds, under continuous far-red light, (□) at 25°C, (■) at 37.5°C.

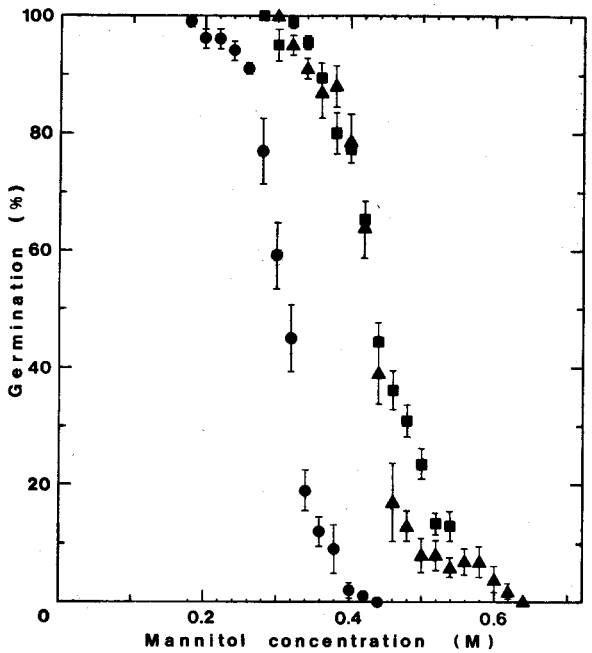

Figure 4. Final germination percentage at 25°C in darkness, for intact (●), opened (■) and decoated (▲) watermelon seeds as a function of the molar concentration of the imbibition medium (mannitol solution). Vertical bars represent 2 SE.

time course curve (Fig. 1), but shifted by 8 h to lower values (the shift being approx. 10.5 h for opened seeds). A similar escape curve was obtained when the seeds were initially imbibed in water prior to mannitol; the shift from the germination curve was nearly 6 h. The four sigmoid curves shown in Fig. 5A were considered as cumulative normal distributions, and the best fits for the corresponding distributions were obtained by the least-sum-of-squares method; their respective means (μ) and variances (σ^2), in h and h^2 are for (A) 21.2 and 4.0; (B) 24.4 and 4.2; (C) 26.3 and 3.3; and (D) 32.2 and 3.8. By using probit transformation of the germination percentages, the sigmoid curves (Fig. 5A) were transformed to linear ones (Fig. 5B). The slopes of the four lines are similar and no statistically significant ($P<0.05$) differences were obtained.

Intermittent, broad-band, far-red illumination (1 or 2 min per 30 min) applied throughout the germination test was fully inhibitory (Fig. 6), but, when each FR pulse was immediately succeeded by an R pulse, full germination was reinstated. When a dark interval was interposed between the two pulses, the final germination percentage depended upon the relative lengths of the dark periods following each R and FR pulse.

Seeds illuminated with continuous or intermittent red light germinated optimally (~100%), when imbibed in water (Table 1 and Fig. 6), but, in mannitol

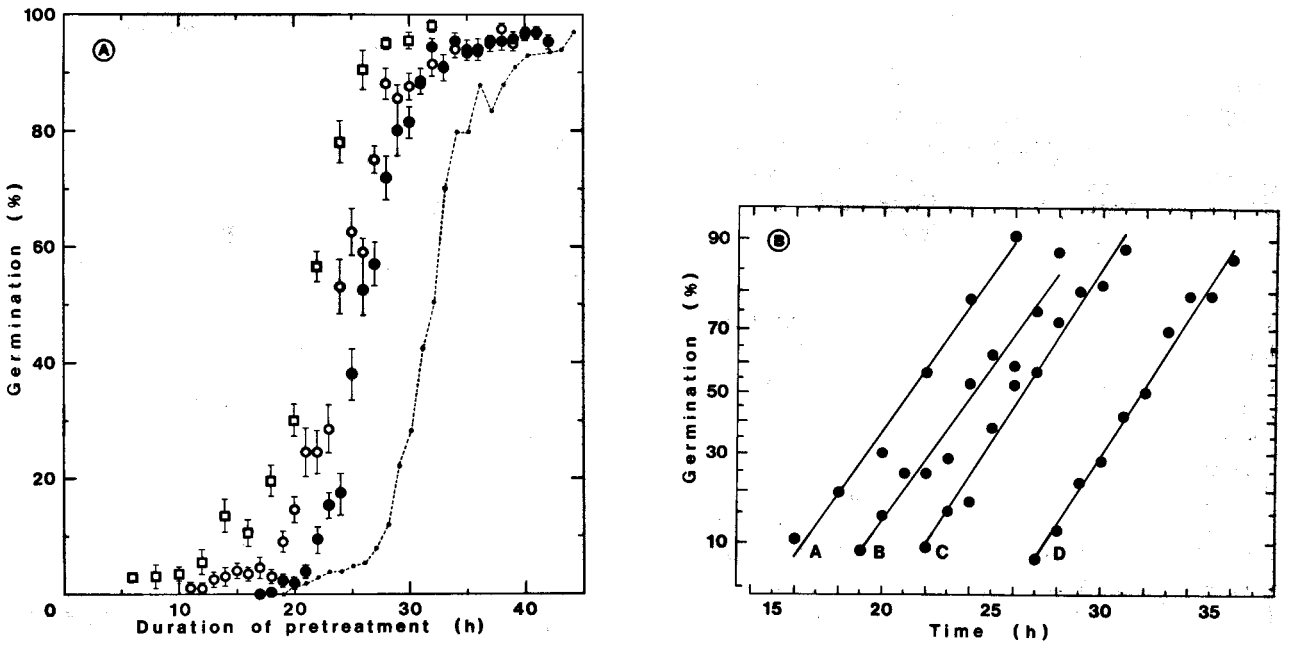

Figure 5. (A) Final germination percentage of watermelon seeds imbibing in 0.5M mannitol solution in darkness (•) or in water and under continuous far-red light ((○) intact seeds, (□) opened seeds) as a function of the duration of a pretreatment period in water and darkness. Temperature was kept throughout at 25°C; (---) time course of dark germination in water throughout (see Fig. 1). Vertical bars represent 2 SE. (B) Probit transformations of the four data sets in (A) and their linear regression curves, given by the following equations:

A, escape of opened seeds from cFR: $Y = -0.624 + 0.264\ X$ ($r^2 = 0.987$, d.f. = 4, $P < < 0.001$);

B, escape of intact seeds from cFR: $Y = -1.315 + 0.261\ X$ ($r^2 = 0.961$, d.f. = 8, $P < < 0.001$);

C, escape from mannitol: $Y = -2.631 + 0.289\ X$ ($r^2 = 0/977$, d.f. = 8, $P < < 0.001$);

D, time course of dark germination: $Y = -4.244 + 0.291\ X$ ($r^2 = 0.987$, d.f. = 8, $P < < 0.001$);

X being time (in h) and Y probit of germination percentage (50% corresponds to probit 5.000).

solutions, germination was considerably lower than in dark controls (Fig. 7). The greater the dose the longer the shift (from the germination potential curve in darkness) towards lower values of osmotic pressure that permit germination: shifts of 0.30, 0.43 and 0.56 MPa were estimated for daily doses of 4.8, 12 and 24 min, respectively, of broad-band red light. In a further experiment, seeds imbibing in a 0.25M mannitol solution (only slightly inhibitory of dark germination, see Figs. 4 and 7) were illuminated with intermittent blue or red monochromatic pulses. All four wavelengths used were considerably inhibitory (Table 3).

Seeds exposed to cFR illumination for various periods (1–5 days) (starting with the onset of imbibition) were subsequently transferred to darkness (Fig. 8). Treatment with cFR for 4 and 5 days did not result in subsequent dark germination; thus, full secondary dormancy had evidently been imposed. On the other hand, treatment for 1 day resulted in only a certain delay of germination (compare with the kinetics of Fig. 1), while 2 and 3 days of cFR imposed partial dormancy. This secondary dormancy was relieved by a short (1 min) R pulse given immediately after the initial 4-day illumination with cFR. A dose–response curve was constructed (not presented) using monochromatic R irradiation (662 nm, photon flux density 8.3 μmol $m^{-2}\ s^{-1}$); a typical sigmoid curve (X axis: log of dose) was obtained, with 50% promotion at approx. 17 s (a dose of approx. 140 μmol

Table 3. Effect of intermittent, blue and red monochromatic illumination on the germination of watermelon seeds, at 25°C

Light treatment (nm)	Germination (% ± SE)
Darkness	91.4 ± 1.0
Blue: 442	48.7 ± 4.3
482	22.7 ± 3.5
Red: 639	15.3 ± 2.2
662	10.7 ± 2.2

Irradiations were given for 1 min every 10 min throughout the experiment. Seeds were imbibing in a 0.25M mannitol solution.

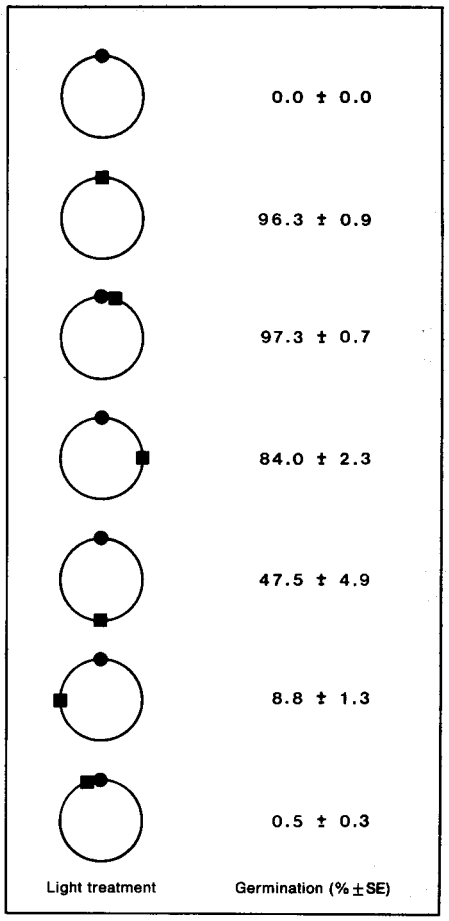

Figure 6. Effect of intermittent red and far-red brief irradiation on the germination of watermelon seeds, at 25°C. Each circle represents a 30-min dark cycle (repeated until final germination percentage was scored) and interrupted by 2-min pulses of red (■) and far-red (●) (11.0 and 18.2 μmol m^{-2} s^{-1}, respectively) the timing of which are shown by the position of the respective symbols in the circles.

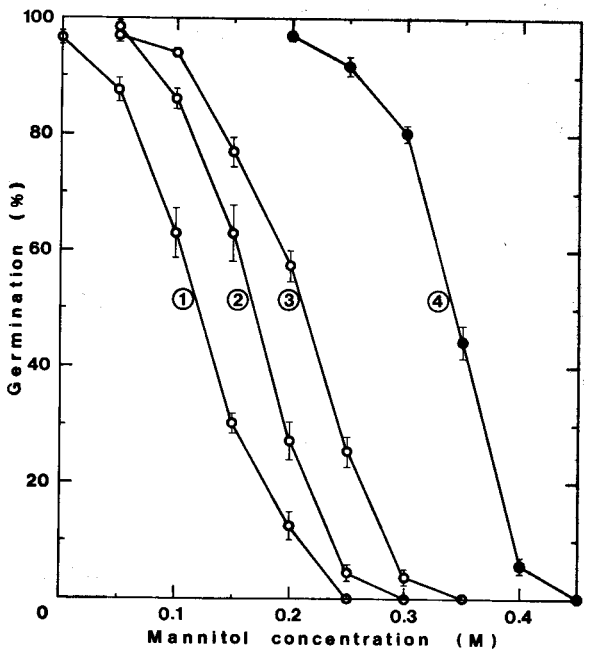

Figure 7. Final germination percentage of watermelon seeds at 25°C under intermittent red light (applied throughout the experiment) as a function of the molar concentration of the imbibition medium (mannitol solution). In curves (1), (2) and (3), 1 min R was given every 1, 2 and 5 h, respectively; curve 4, in darkness. Vertical bars represent 2 SE.

m^{-2}) and nearly 100% germination with approx. 60 s (approx. 500 μmol m^{-2}). Full reversibility of the red effect on the relief of dormancy was shown by a 10-min FR pulse; reversal of the effect of the previous illumination by a consecutive pulse was obtained several times.

Discussion

According to Lorenz and Maynard (1980), optimum soil temperature for germination of watermelon seed ranges from 21.3 to 35.3°C; 15.7°C is the minimum at which germination has been reported. Optimal dark germination for the seeds of the cultivar Sugar Baby has been found (Sachs, 1977) to occur in the range 15–35°C. The present data for Sugar Baby support both statements; the range of optimal temperature was somewhat enlarged, extending from 20 to 40°C, while minimum temperature was certainly below 15°C (Fig. 2). Moreover, the germinability curve of opened seeds under cFR (Fig. 2) leads, though indirectly, to the conclusion that 37.5°C is the optimum temperature of germination. This range of high temperatures for germination is consistent with the subtropical origin of the species; wild-grown watermelon is a summer annual, indigenous of southern African arid and semi-arid habitats (Botha *et al.*, 1982a).

The watermelon seeds used in this study should be characterized as absolute dark germinators. The inhibitory action of cFR, intermittent FR, cB and white incandescent light was evident by the suppression of final germination, while in mannitol solutions the influence of R light was also unfavourable (Fig. 7, Table 3). Although the inhibition of germination appears to require long periods of irradiation, as reported for various species of the Cucurbitaceae, germination can also be suppressed by intermittent FR. Moreover, when each FR pulse was followed by an R pulse, germination was restored. Similarly, the dormancy that had been imposed by 4 or 5 days of cFR was shown to be under typical, R/FR reversible, phytochrome control. All these results lead to the conclusion that germination in Sugar Baby water-

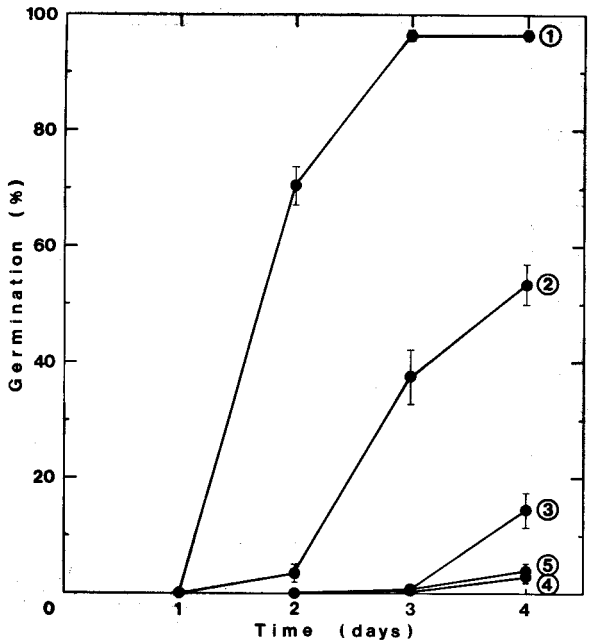

Figure 8. Time courses of dark germination for watermelon seeds illuminated (from the onset of imbibition) with continuous far-red light for 1, 2, 3, 4 and 5 days (curves 1–5, respectively) before transfer to darkness (time 0). Temperature was kept throughout at 25°C. Vertical bars represent 2 SE.

melon is controlled by the low-energy reaction of phytochrome, consistent with reports by Botha *et al.* (1982a,b) on wild-grown watermelon and by Loy and Evensen (1979) on the dwarf watermelon strain WB-2, as well as with the much earlier work on cucumber (Yaniv *et al.*, 1967).

Nakamura *et al.* (1955) have found that, in several cucurbitaceous seeds, decoating did not remove photosensitivity; in certain cases, it even augmented it (probably as a result of the increased light flux density reaching the embryo). On the other hand, numerous studies have shown that removal of embryo-covering structures enhances germinability (Bewley and Black, 1982). The removal of the lignified testa in wild-grown watermelon seeds (Botha *et al.*, 1982a) only slightly reduced white-light inhibition, but the additional removal of the inner membrane resulted in full germination in the light. The conclusion from the present study is that the outer, lignified part of the testa in Sugar Baby watermelon seeds exerts a restrictive, mechanical action upon the expanding radicle of a force calculated to be approx. −0.30 MPa (Fig. 4). The inner, membranous covering could not be removed without damage to the embryo and, therefore, its inhibitory action could not be assessed.

By comparing germination in seeds from wild-grown plants and the cultivated Sugar Baby, one finds higher 'vigour' in the latter. This is illustrated by the higher rate of germination in Sugar Baby; full germination was obtained in <48 h at 25°C (Fig. 1) as opposed to 96 h at 27°C, for the wild-grown seeds (Botha *et al.*, 1982a). Germination in the latter was extremely sensitive to water stress (Botha and Small, 1988); an osmotic potential of −0.12 MPa suppressed germination by 50%, and −0.43 MPa was completely inhibitory, while effective potential values were considerably lower in Sugar Baby (−0.74 and −1.08 MPa, respectively, Fig. 4).

By comparing the escape curves (Fig. 5), it can be seen that phytochrome activation precedes activation of radicle elongation by a short period (approx. 2 h). Furthermore, taking into consideration the three-phased pattern of the imbibition kinetics (Fig. 1), it is interesting that the cFR-irreversible, phytochrome-mediated activation of germination and the osmotically irreversible activation of radicle elongation coincide largely with the second stationary phase of water uptake (20–30 h after sowing); this is illustrated by the probit curves (Fig. 5B), where 10–90% of the seeds were irreversibly activated 18–32 h after the onset of imbibition. It is therefore concluded that, during the second stationary phase of water uptake, activation of germination takes place in watermelon.

A further interesting feature is the effect of red light. Previous results have shown a reduced rate of germination under cR (Loy and Evensen, 1979; Botha and Small, 1988). Botha and Small (1988) showed partial inhibition of germination by intermittent broad-band and monochromatic red irradiation. In the present study, a negative effect of R light was shown in all three types of R treatments applied (i.e. broad-band R, continuous and intermittent, and monochromatic intermittent R); even though germination in water was always nearly 100%, the inhibitory action of R light was revealed (Fig. 7 and Table 3) as a considerable decrease in the germination potential curve (i.e. of the germinability as a function of the osmotic potential of the imbibition medium). Thanos (1984) has also shown that the pre-germination pool of total free amino acids in the radicles of watermelon seeds was significantly lower in cR than in dark controls. The interpretation of the inhibitory action of R light is not clear. Recent findings have attributed the inhibitory action of R and white light on germination to the prevention of the action of existing phytochrome P_{fr} (due to P_{fr} destruction or P_{fr} unavailability) that might be caused by high rates of 'cycling' through the different molecular forms of phytochrome (Bartley and Frankland, 1982; Taylorson, 1991; Thanos *et al.*, 1991). Nevertheless, the considerable inhibition caused by a daily dose of iR of <5 min (Fig. 7) could not be explained by the cycling concept. Alternative interpretations would be P_{fr} destruction and/or decrease of φ (i.e.

$[P_{fr}]:[P_{tot}]$ by R, and this could happen only if the seeds imbibing in the dark have a φ of >0.8.

Acknowledgments

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