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ORIGINAL ARTICLE

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The *7B-1* mutant in tomato shows blue-light-specific resistance to osmotic stress and abscisic acid

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Abstract Germination of wild-type (WT) tomato (*Lycopersicon esculentum* Mill.) seed is inhibited by mannitol (100–140 mM) in light, but not in darkness, suggesting that light amplifies the responsiveness of the seed to osmotic stress (M. Fellner, V.K. Sawhney (2001) Theor Appl Genet 102:215–221). Here we report that white light (W) and especially blue light (B) strongly enhance the mannitol-induced inhibition of seed germination, and that the effect of red light (R) is weak or nil. The inhibitory effect of mannitol could be completely overcome by fluridone, an inhibitor of abscisic acid (ABA) biosynthesis, indicating that mannitol inhibits seed germination via ABA accumulation in seeds. The inhibition of WT seed germination by exogenous ABA was also amplified by W or B, but not by R. In a recessive, ABA-overproducing, *7B-1* mutant of tomato, seed germination and hypocotyl growth were resistant to inhibition by mannitol or exogenous ABA, both in W or B. Experiments with fluridone suggested that inhibition of hypocotyl growth by W or B is also partially via ABA accumulation. De-etiolation in the mutant was especially less in B compared to the WT, and there was no difference in hypocotyl growth between the two genotypes in R. Our data suggest that B amplifies the responsiveness of tomato seeds and hypocotyls to mannitol and ABA, and that W- or B-specific resistance of the *7B-1* mutant to osmotic stress or ABA is a consequence of a defect in B perception or signal transduction.

Keywords Abscisic acid · Blue light · Germination · Hypocotyl growth · *Lycopersicon* (*7B-1* mutant) · Osmotic stress

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Abbreviations ABA: abscisic acid · B: blue light · BM: basal medium · fluridone: 1-methyl-3-phenyl-5-[3-trifluoromethyl-(phenyl)]-4(1*H*)-pyridinone · FR: far-red light · LD: long day · R: red light · W: white light· WT: wild type

Introduction

In field conditions, plants are often exposed to various abiotic stresses such as dehydration, low temperature, and high salinity. Since the effects of such factors are due at least in part to impaired water absorption and transport, they are considered to be different forms of osmotic stress (Ryu et al. 1995; Xiong et al. 1999). Abiotic stresses substantially reduce crop plant productivity (Epstein et al. 1980). Therefore, an understanding of the underlying mechanisms involved in the plant responses to abiotic stresses is essential to solve this important agronomic problem.

One possible mechanism by which plants resist abiotic stresses is via the accumulation of abscisic acid (ABA; Goldbach and Michael 1976; Mäntylä et al. 1995). The pivotal role of ABA in plant responses is shown in ABA-deficient mutants that are impaired in tolerance to abiotic stresses (Koornneef et al. 1982; Bray 1988; Heino et al. 1990; Chen and Plant 1999), and by the reversal of this defect with exogenous ABA (Heino et al. 1990). Also, in many species ABA treatment makes plants more resistant to abiotic stresses (Chen and Gusta 1983; LaRosa et al. 1987), and several ABA-response genes are induced in response to an abiotic stress (Hahn and Walbot 1989; Yamagushi-Shinozaki et al. 1989).

In plant tissues, the levels of several hormones, including ABA, are altered by light conditions (Kraepiel and Miginiac 1997). Feldman et al. (1985) and Leopold and La Favre (1989) showed that red light (R) treatment leads to an increase in ABA in maize roots. In contrast, R decreases endogenous ABA levels in germinating lettuce seeds (Toyomasu et al. 1994). Similarly, R-induced negative regulation of ABA levels was shown in vegetative

tissues of *Lemna* and *Arabidopsis* (Weatherwax et al. 1996, 1998). In a phytochrome-deficient mutant of *Nicotiana* the increase in endogenous ABA levels was related to R-controlled ABA degradation (Kraepiel et al. 1994).

The level of endogenous ABA is also regulated by blue light (B). Blue-light-induced inhibition of hypocotyl elongation in *Lactuca* corresponded with high concentrations of ABA (Volmaro et al. 1998) and, in *Prunus*, B resulted in increased endogenous ABA compared with R treatment (Baraldi et al. 1995). When B was combined with R or far-red light (FR), the ABA level declined. These results suggest that B and R may interact with each other in the modulation of endogenous ABA in plant tissues. The fact that light has a role in the biosynthesis/metabolism of ABA raises the question of the role of light in plant responses to abiotic stresses. It has been suggested that light may affect the sensitivity of tissues to plant hormones, such as gibberellins (Reed et al. 1996) or brassinosteroids (Szerkes et al. 1996). However, to the best of our knowledge, no information is available on whether light affects tissue sensitivity to osmotic stress and ABA.

We recently reported that in white light (W) under long days (LDs), seed germination in the *7B-1* mutant of tomato is resistant to abiotic stresses, including osmotic, salt and low-temperature stresses (Fellner and Sawhney 2001). We also showed that in LDs, *7B-1* seedlings exhibit reduced de-etiolation of hypocotyls, and that the mutant hypocotyls contain elevated levels of endogenous ABA, relative to the WT (Fellner et al. 2001). Here we report that in continuous W or B, but not in R, the *7B-1* mutant exhibits, relative to the WT, enhanced resistance to mannitol and exogenous ABA as evidenced by increased seed germination and relatively greater hypocotyl growth. The results presented suggest that in the *7B-1* mutant of tomato there is a defect in B perception or signal transduction.

Materials and methods

Plant material and growth conditions

The *7B-1* mutant was isolated as a male-sterile line of tomato (*Lycopersicon esculentum* Mill., background, cv. Rutgers ; Sawhney 1997). For all experiments, *7B-1* and wild-type (WT) seeds were obtained from plants grown under a short-day (SD) photoperiod (8 h light/16 h dark) in a growth chamber with a temperature regime of 25 °C light/23 °C dark. Light was provided by fluorescent tubes (F72T12/CW/VHO; Sylvania, USA) and incandescent bulbs (Long Life 7500 h; Litemor, Canada) at a photon flux density (PFD) of 90–200 μmol m^{-2} s^{-1}.

Germination tests

Seeds were surface-sterilized by soaking in 50% (v/v) Javex-5 solution (3% sodium hypochlorite; Colgate-Palmolive Canada, Toronto, Canada) for 25 min, and rinsed extensively with sterile distilled water. *7B-1* and WT seeds were germinated 30–40 seeds per Petri dish. The basal medium (BM) contained Murashige and Skoog (1962) salts, 1% (w/v) sucrose, 1 mM Mes, and 0.7% (w/v) agar (pH adjusted to 6.1 by KOH before autoclaving) with or without different concentrations of mannitol (Fisher Scientific, Fair Lawn, N.J., USA), abscisic acid [(±)-cis,trans-ABA; Sigma, St. Louis, Mo., USA), or fluridone (1-methyl-3-phenyl-5-[3-trifluoromethyl-(phenyl)]-4(1*H*)-pyridinone; Eli Lilly, Indianapolis, Ind., USA). Mannitol, ABA, as well as fluridone were added to the medium by sterile filtration (0.22 μm Millex-GS filter unit; Millipore Co., Bedford, Mass., USA) after autoclaving. Petri dishes with seeds were placed in an incubator set at 25 °C, either in darkness or in continuous W, B, R, or FR (for filters used see below). Seed germination, defined as radicle protrusion, was scored from 2–20 days after sowing.

Hypocotyl growth

One day after germination in the dark, *7B-1* and WT seeds were transferred either to new BM in Petri dishes, or to BM supplemented with ABA, fluridone or mannitol. The dishes with seeds were vertically aligned and then placed under W, B, R, or FR, or kept in the dark. After 5–12 days, the hypocotyl length was measured.

Light sources

White light was provided by white fluorescent tubes (F20T12/CW; Sylvania) with a PFD of 25–40 μmol m^{-2} s^{-1}. Blue light was provided by filtering light from a white fluorescent tube through three layers of blue Roscolux membrane (#83; Rosco, Port Chester, N.Y., USA) with a PFD of 4 μmol m^{-2} s^{-1}. Red light was provided by filtering light from a white fluorescent tube through three layers of red Roscolux membrane (#27) with a PFD of 5 μmol m^{-2} s^{-1}. Far-red light was provided by filtering light from a 500-W incandescent lamp (Philips Lighting Company, Somerset, N.J., USA) through a Plexiglas FR filter (FRF 700; Westlake Plastic Company, Lenni, Pa., USA) with PFD 13 μmol m^{-2} s^{-1}. PFDs of W, B and R were measured with a quantum photometer (model Li-185B; Li-Cor, Lincoln, Neb., USA) and PFDs of FR were measured with portable spectroradiometer (model LI-1800; Li-Cor).

Results

Seed germination

In the control, i.e. on BM, there were no major differences in the germination rate and percent germination between the WT and *7B-1* mutant seeds in the dark, W, R, or in B (Fig. 1a–d). FR almost completely inhibited seed germination in WT and in *7B-1* (Fig. 1e). However, when seeds were transferred from FR to W or the dark, germination was fully restored in both genotypes, 4–5 days after the transfer (Fig. 1e).

We previously reported that the osmotica mannitol and polyethylene glycol (PEG) inhibit seed germination in the WT and in the *7B-1* mutant in light (in LDs), and that *7B-1* seeds are resistant to the inhibitory effect of the two osmotica in light (Fellner and Sawhney 2001). Here we examined the resistance of mutant seeds to mannitol in different parts of the light spectrum. As shown earlier (Fellner and Sawhney 2001), mannitol (100–140 mM) did not inhibit germination in the dark in either WT or *7B-1* seeds . Light amplified the responsiveness of tomato seeds to mannitol but to a different extent in WT and *7B-1*. Under W, mannitol (100–140 mM) inhibited WT seed germination by approximately 50% to almost

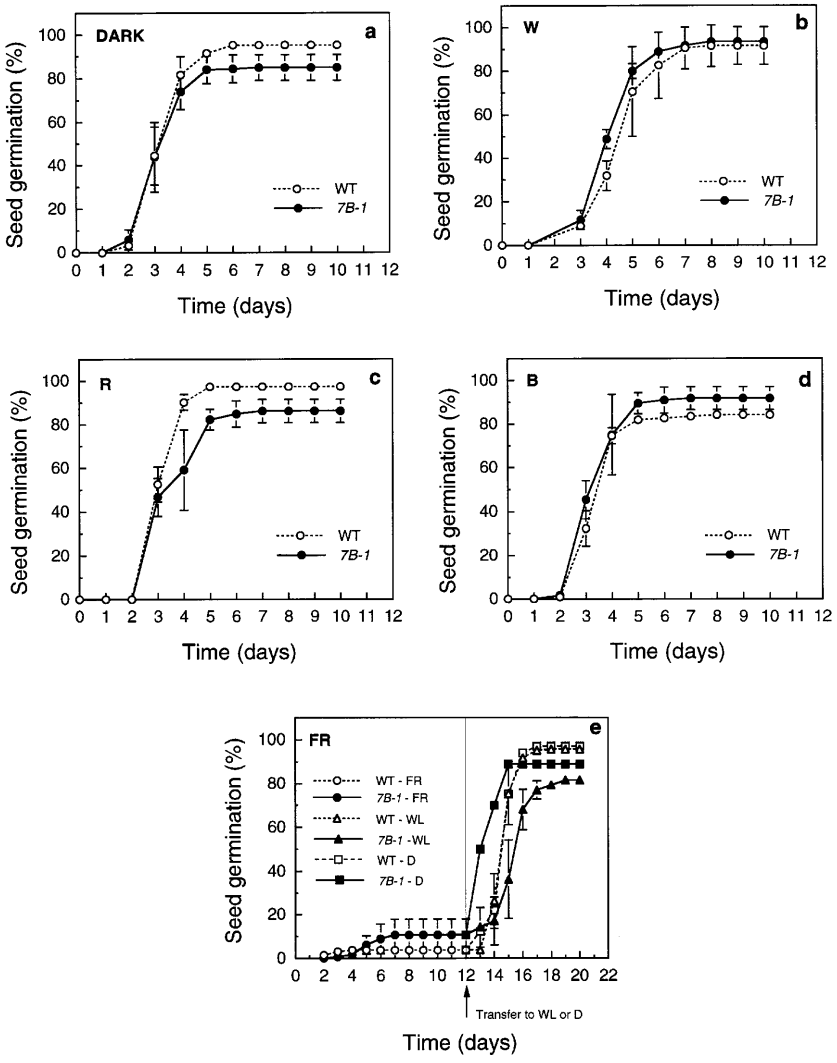

Fig. 1 Kinetics of seed germination in WT tomato (*Lycopersicon esculentum*) and the *7B-1* mutant on BM in darkness (**a**), W (**b**), R (**c**), B (**d**) or FR (**e**). For each genotype and light condition, at least 30 seeds were scored for germination. Each value represents the mean ± SE of three independent experiments. In the case of FR (**e**), germination of seeds after transfer from FR to darkness represents data from one experiment

100%, compared to the control (Fig. 2a). In contrast, seed germination in *7B-1* was unaffected at low (100 mM), and reduced to 50% in high (140 mM), mannitol concentrations (Fig. 2a). Red light had a weak effect on the WT seed germination response to mannitol, although at 140 mM it strongly inhibited it and the effect was less in the *7B-1* mutant (Fig. 2b). The most striking difference between WT and *7B-1* responses to mannitol was observed in B. Mannitol strongly inhibited WT seed germination, whereas *7B-1* seeds were almost completely insensitive to mannitol (Fig. 2c).

A comparison of WT and *7B-1* seed germination in the dark and B in the presence of different concentrations of mannitol is shown in Fig. 3a.

We then examined the possibility that mannitol-xinduced inhibition of germination in W or B is caused by ABA accumulation. WT and *7B-1* were germinated in the presence of mixtures of mannitol and fluridone (10 μM), an inhibitor of ABA biosynthesis (Gamble and Mullet 1986; Saab et al. 1990; Xu and Bewley 1995). Whatever the light quality, fluridone completely restored germination from the inhibitory effect of mannitol in both the genotypes (Figs. 2, 3b).

Next we examined the effects of exogenous ABA on seed germination with respect to light quality. In the dark as well as in W, exogenous ABA inhibited germination in both WT and *7B-1* seeds, although inhibition was greater in light than in darkness (Fig. 4a, b). In light, the extent of ABA-induced inhibition was dependent on light quality. In R, as in the dark, WT and *7B-1* showed similar sensitivity to ABA with 50% inhibition induced by approximately 6×10^{-6} to 1×10^{-5} M ABA (Fig. 4a, c). In continuous W, WT and *7B-1* seeds responded similarly to ABA (Fig. 4b) although less ABA was needed for 50% inhibition than in darkness or R (Fig. 4a, c). The major difference between WT and *7B-1* seeds occurred in B, where germination of *7B-1* seeds was strongly resistant to ABA relative to the WT, except at high (10^{-5} M) concentration (Fig. 4d).

Hypocotyl elongation

Blue-light-specific resistance of *7B-1* mutant seed germination to mannitol or ABA led us to hypothesize that *7B-1* seedling growth may also be less sensitive to B.

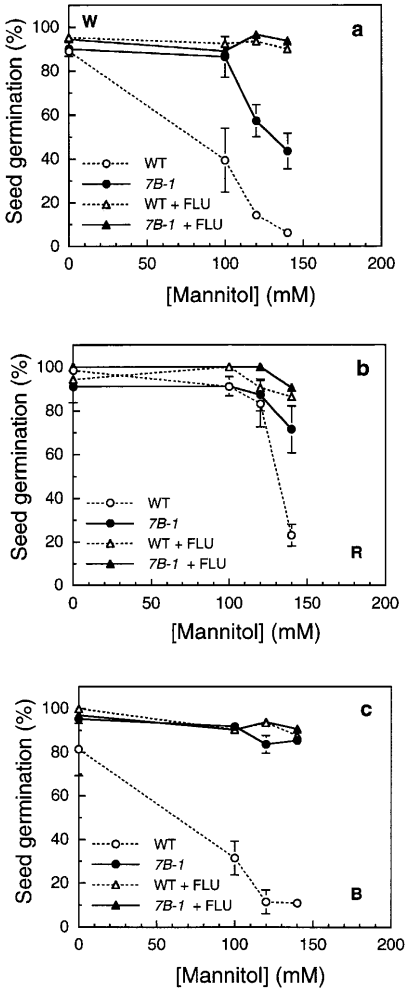

Fig. 2 Germination of seeds of WT and *7B-1* mutant tomato in the presence of mannitol with or without fluridone (*FLU*; 10 μM) in W (**a**), R (**b**) or B (**c**). For each genotype and light condition at least 30 seeds were scored for germination 10 days after sowing. Values represent mean ± SE of three independent experiments

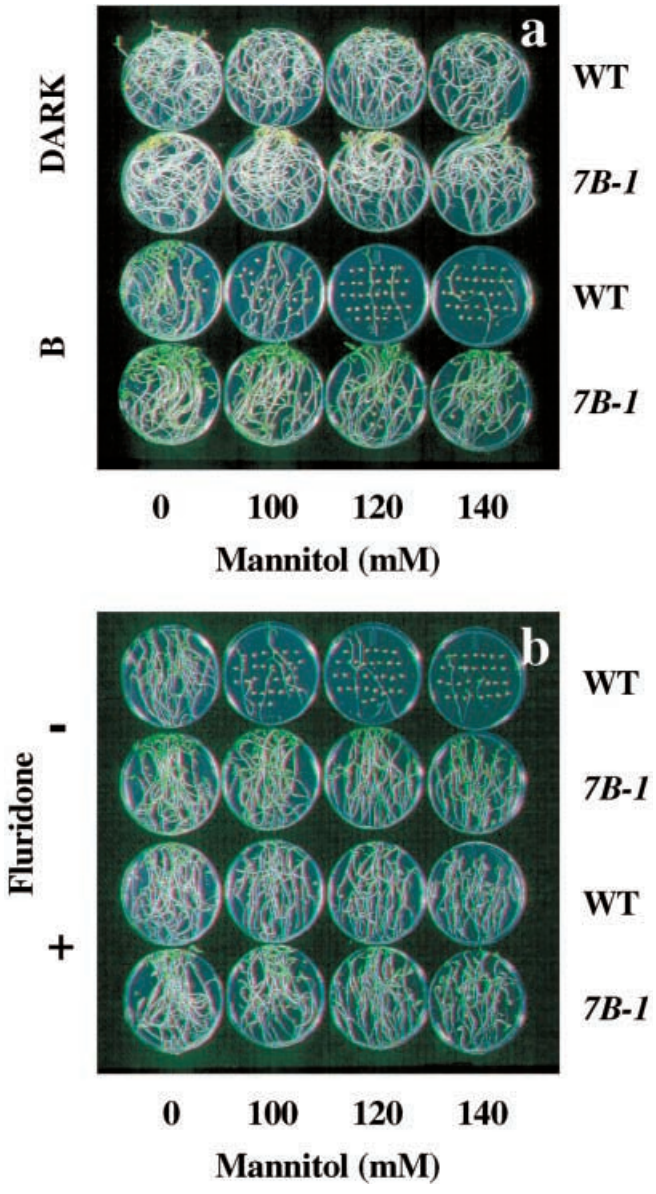

Fig. 3 Effect of darkness or B (**a**) or fluridone (10 μM) (**b**) on the germination of seeds of WT and *7B-1* mutant tomato in the presence of different concentrations of mannitol. Each treatment in **a** represents germination after 10 days and in **b** after 7 days of sowing. Values represent mean seed germination ± SE of three independent experiments

Therefore, we examined the growth of WT and mutant hypocotyls reared on a BM in various light conditions. In the dark, there was no difference between *7B-1* and WT hypocotyls, and R inhibited hypocotyl growth to a similar extent in both genotypes (Fig. 5a). In FR, *7B-1* hypocotyls showed slightly less de-etiolation, i.e. inhibition of growth, than those of the WT (Fig. 5a). However, de-etiolation of *7B-1* hypocotyls, compared to WT, was relatively much less in W, and especially in B (Fig. 5a).

We previously reported that, in W, fluridone (0.1–1 μM) significantly stimulates hypocotyl elongation in WT but not in *7B-1* seedlings (Fellner et al. 2001). Fluridone did not affect hypocotyl growth in WT or *7B-1* seedlings in the dark, R or FR (data not shown). However, under B, distinct differences occurred between WT and *7B-1* hypocotyl growth in the presence of fluridone. In the WT, fluridone stimulated hypocotyl growth but in the mutant it was unaffected (Fig. 5b).

The resistance of the mutant hypocotyl to B-induced inhibition led us to investigate the responsiveness of hypocotyl growth to mannitol and ABA under different light conditions. Mannitol (140 mM) inhibited hypocotyl growth in tomato seedlings in the dark as well as in light and, as in seed germination, WT and *7B-1* hypocotyls exhibited similar responses in darkness or R (Fig. 6a, b). However, mannitol-induced inhibition of mutant hypocotyl growth in B was relatively much less (approx. 17%) compared with the WT (approx. 30%; Fig. 6c). Similarly in B, mutant hypocotyls showed less sensitivity to the inhibitory effect of exogenous ABA than the WT. At 3 or 5 μM ABA, WT hypocotyls were

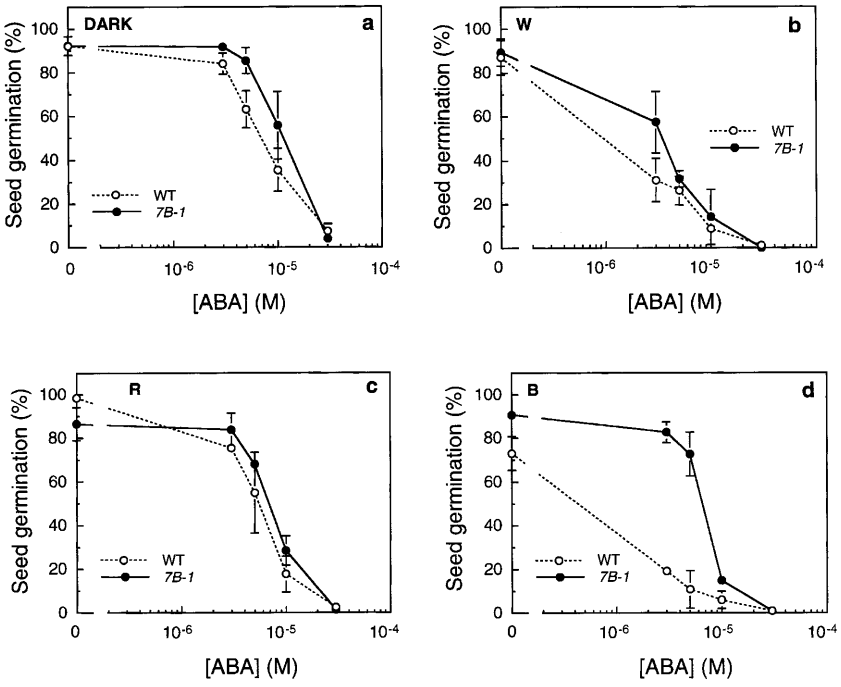

Fig. 4 Germination of WT and *7B-1* mutant tomato seeds in the presence of exogenous ABA in the dark (**a**), W (**b**), R (**c**) or B (**d**). For each genotype and light condition at least 30 seeds were scored for germination 9 days after sowing. Values represent mean ± SE of three independent experiments

approx. 40% shorter than the control seedlings, whereas at the same concentrations, the inhibition in *7B-1* mutant hypocotyls was approximately 16% (Fig. 7).

Discussion

In some systems, including tomato, plant tissues respond to abiotic stresses by increasing endogenous ABA (Goldbach and Michael 1976; Daie and Campbell 1981; Chandler and Robertson 1994; Mäntylä et al. 1995). In WT and *7B-1* mutant tomato seeds, the ability of fluridone to overcome the inhibitory effect of mannitol on germination (Fig. 2) indicates that high osmoticum-induced inhibition of germination is via accumulation of endogenous ABA. We previously reported that various abiotic stresses inhibit seed germination in tomato in light (in LDs), but not in darkness, indicating that light somehow amplifies the inhibitory effect of the abiotic stress (Fellner and Sawhney 2001). In this study, we report that continuous W or B strongly amplifies the ability of mannitol to inhibit germination in WT seeds, and that B has a stronger effect than W (Figs. 2, 3). In contrast, R had a weak or nil effect on mannitol-induced inhibition.

One possible mechanism by which B may amplify the inhibition of germination by mannitol in WT tomato seeds is that it stimulates the mannitol-induced ABA accumulation in seeds. This is supported by the observation that the inhibition of germination in WT seeds by exogenous ABA is also maximal in B compared to darkness or R (Fig. 4). Blue light has been shown to increase the level of endogenous ABA in some systems (Baraldi et al. 1995) and R is positively involved in ABA degradation (Kraepiel et al. 1994). Thus, it is possible that similar mechanisms operate in tomato seeds.

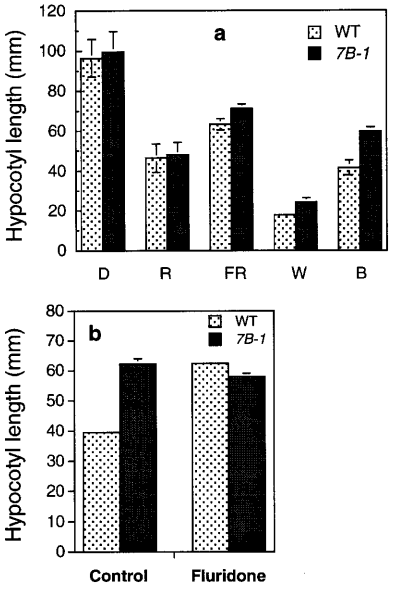

Fig. 5 Hypocotyl length in WT and *7B-1* seedlings of tomato grown on BM in the dark, W, B, R or FR (**a**), or grown in B in the presence of fluridone (10 μM) (**b**). Length of hypocotyl was measured 7 days after germination. Values represent mean ± SE of 60 seedlings from three independent experiments, and in the case of B in **a**, 80 seedlings were measured from four independent experiments

We earlier reported that seed germination in the *7B-1* mutant is strongly resistant to various abiotic stresses in comparison to the WT in W (in LDs), but not in the dark (Fellner and Sawhney 2001). Here, we show that the resistance of *7B-1* seeds to mannitol or exogenous ABA is specifically pronounced in B. High germination in *7B-1* seeds in B in the presence of mannitol or

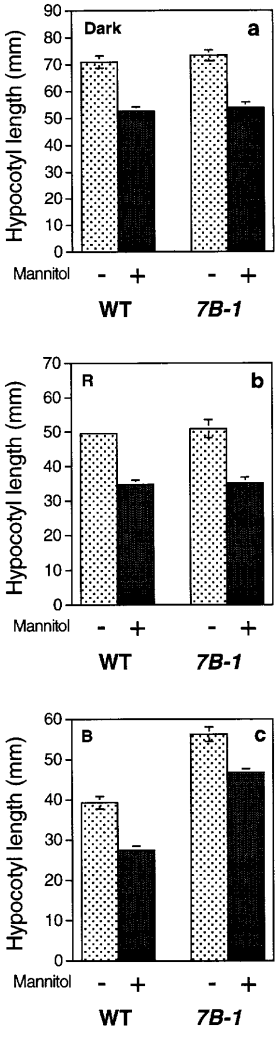

Fig. 6 Hypocotyl lengths in WT and *7B-1* seedlings of tomato grown in the presence or absence of mannitol (140 mM) in the dark (**a**), R (**b**) or B (**c**). Values represent mean ± SE of 60 seedlings from three independent experiments. Hypocotyl length was measured after 5 days (in darkness) or 7 days (in R or B) of seed germination

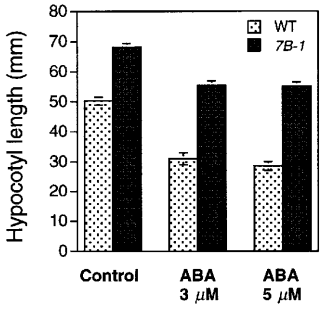

Fig. 7 Hypocotyl lengths of 7-day-old WT and *7B-1* tomato seedlings grown in the presence of ABA (3 μM or 5 μM) under B. Values represent mean ± SE of 60 seedlings from three independent experiments

exogenous ABA, at concentrations inhibitory for WT seeds, could be due to reduced level of endogenous ABA in *7B-1* seeds. Analysis of endogenous ABA in WT or *7B-1* seeds was not performed. However, our earlier results suggested that *7B-1* seeds contain more, not less, endogenous ABA than WT seeds (Fellner at al. 2001). Thus, it is likely that B regulates the responsiveness of WT seeds to mannitol and ABA by increasing seed sensitivity to ABA. This suggestion is supported by data from experiments on hypocotyl growth.

Hypocotyl growth in the *7B-1* mutant exhibited reduced de-etiolation, relative to the WT, in W or B, but not in R or FR (Fig. 5a), indicating that *7B-1* hypocotyls are specifically less sensitive to B. Earlier we showed that *7B-1* hypocotyls contain higher levels of endogenous ABA than the WT in W (Fellner et al. 2001). Analysis of endogenous ABA in WT and *7B-1* hypocotyls grown under B has not been performed. However, in B as in W, fluridone, an inhibitor of ABA biosynthesis, stimulated hypocotyl growth in the WT but not in *7B-1* (Fig. 5b). This suggests that endogenous ABA in B-grown mutant hypocotyls is also at a higher level than in WT, and that ABA is involved, at least partially, in W- and B-induced inhibition of hypocotyl growth. This is consistent with the observation that exogenous ABA inhibits hypocotyl elongation (Fig. 7; Fellner et al. 2001). However, even though *7B-1* hypocotyls contain an elevated level of endogenous ABA in W, and possibly in B, they show reduced de-etiolation and less growth inhibition by mannitol or ABA in W or B (Figs. 6, 7). Taken together, the data indicate strongly that in the *7B-1* hypocotyl, sensitivity to endogenous ABA is reduced in B or W, as compared to WT, and is consistent with the deduced lower sensitivity to B of *7B-1* mutant seed germination. Thus, we propose that B-specific resistance of *7B-1* seed germination and hypocotyl elongation to osmotic stress and ABA is primarily due to a defect in B perception or signaling.

In Fig. 8, we present a working model which attempts to explain the mechanisms by which B signaling affects tissue sensitivity to ABA in seed germination and hypocotyl growth. It is proposed that, in the WT, B increases tissue sensitivity to ABA (receptor X), which in turn results in a reduction in the endogenous ABA level. ABA is perceived by receptor X, and the signal is further transduced with negative effects on the expression of hydrolytic-enzyme genes induced by gibberellic acid, resulting in the inhibition of seed germination. ABA is also perceived by another receptor, Y (not directly influenced by B), and the signal induces expression of genes involved in the biosynthesis of osmolytes needed for osmotic tolerance; in the WT, the expression is reduced and there is less tolerance to the osmotic stress. In the *7B-1* mutant, a defect in B perception/transduction results in less sensitivity to B and consequently reduced sensitivity of receptor X to ABA (fewer receptors or their modification), and high levels of endogenous ABA. Thus, there is less inhibition of the gibberellin-induced pathway in the *7B-1* mutant and less inhibition of germination. At the same time, high levels of ABA in *7B-1* seeds would bind to more Y receptors

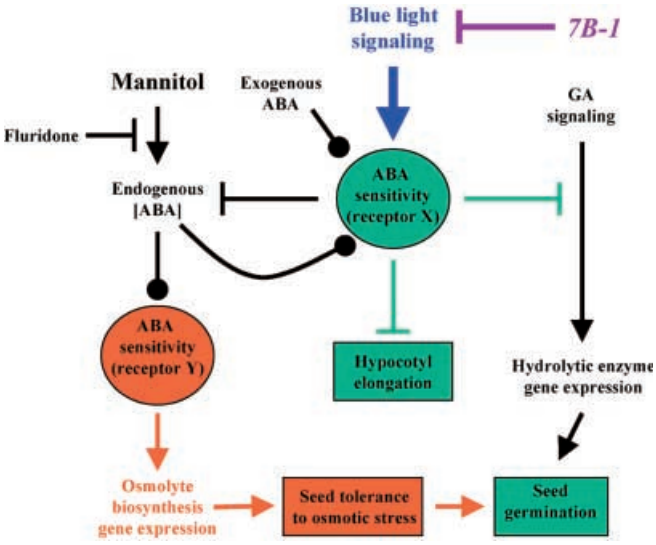

Fig. 8 A working model showing the effect of blue light on ABA signaling in WT and *7B-1* mutant tomatoes in relation to seed germination and hypocotyl elongation under osmotic stress or in the presence of exogenous ABA. *Arrows* and *T-bars* represent positive and negative effects, respectively. Hormone binding is shown by *lines ending with a dot*

resulting in enhanced expression of genes involved in osmolyte production and, thus, increased tolerance to osmotic stress. For WT hypocotyl growth, B-induced increased sensitivity to ABA negatively affects hypocotyl growth, and in the mutant reduced sensitivity to ABA leads to increased hypocotyl growth.

To simplify the model, the effect of R in seed germination and hypocotyl growth is not included. In contrast to B, R had a weak effect on the responsiveness of *7B-1* seeds to mannitol, indicating an interaction between R and B in the induction of responsiveness to osmotic stress. Thus, the *7B-1* mutant seems to be an interesting system for the study of B and R interaction in the regulation of ABA biosynthesis/metabolism and sensitivity.

In conclusion, we suggest that B increases tissue sensitivity to ABA and that the *7B-1* mutant is less sensitive to B than the WT. To our knowledge, this is the first report showing that B amplifies the responsiveness of seed germination and hypocotyl growth to mannitol or ABA, and emphasizes the importance of B in the control of plant responses to osmotic stress.

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