



Research article

Effects of drying rates on quality of Thai hot-chili (*Capsicum annuum* L.) seed after priming

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Abstract

The effect of drying rates was investigated on the quality of Thai hot-chili (*Capsicum annuum* L. cv Maeping) seeds that were primed using 2% KNO₃ solution at 20°C for 72 hr followed by eight drying treatments: 1) rapid drying (RD) by drying primed seeds at 35% relative humidity (RH) for 72 hr, 2–7) slow drying (SD) by drying primed seeds at 75% RH for 12 hr, 24 hr, 36 hr, 48 hr, 60 hr or 72 hr, respectively, followed by RD treatment as previously described and 8) double slow drying (DSD) by drying primed seeds at 75% RH for 48 hr followed by 50% RH for 48 hr and then RD. The seed quality was assessed based on a germination test, an emergence test, a controlled deterioration (CD) test and headspace ethanol assay. The results showed that all drying treatments significantly improved the germination rate and emergence performance of primed seed compared to the control. SD ≥ 48 hr and DSD outperformed RD for all seed quality determined. On the contrary, the germination rate and field emergence performance of SD ≥ 48 hr and the DSD treatments decreased significantly after the CD test. The negative effect of these slow-drying treatments on seed vigor was confirmed by their significant increases in headspace ethanol production after CD testing compared to RD. The optimum drying treatment is to dry the primed seed at 75% RH and 20°C for 12 hr, followed by rapid drying at 35% RH and 20°C for 3 d.

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Introduction

For the last two decades, commercial seedling use for vegetable crop production has increased worldwide, since this helps farmers save time and labor for seedling preparation and the cultivation time can occur as planned (Cantliffe, 2009). Consequently, the demand has risen for quality vegetable seeds with high rates and uniformity of germination that are suitable for commercial seedling production (Kubota, 2008). Various post-harvest methods have been developed to enhance seed quality. One of the methods used for improving the rate and uniformity of seed germination is the seed priming, a technique that controls seed imbibition and allows pregerminative metabolism to occur to some extent while also prohibiting radical emergence, so that when the primed seeds reabsorb moisture, they germinate more quickly and more uniformly than unprimed seeds (McDonald, 1998).

Despite the advantage of seed priming, its application in the seed production industry is still limited. One of its major drawbacks is the rapid loss of the longevity of primed seeds during storage (Powell et al., 2000; Demir, 2003). It was hypothesized that the priming process caused seeds to reach the state of germination advancement where they lose desiccation tolerance (Sliwinska and Jendrzejczak, 2002) or become less able to resist damage during air-dry storage (Powell et al., 2000). Slow drying has been reported as a post-priming drying treatment to alleviate the negative effect of seed priming with conventional rapid drying in lettuce (Schwember and Bradford, 2005), celery (*Apium graveolens* L.; Coolbear et al., 1992), pansies (*Viola × wittrockiana*; Bruggink et al., 1999), and tomato (*Lycopersicon esculentum* Mill.; Gurusinghe et al., 2002). In contrast, the negative effect of slow drying on longevity during primed seed storage was found in bitter melon (Lin et al., 2005) while both rapid and slow drying made no difference in the storage potential for pepper and pansy seeds (Bruggink et al., 1999). This inconsistent effect of slow drying on the quality and longevity of primed seeds may have been caused by different responses of different seed kinds or by the different rates of drying used or both (Girolamo and Barbanti, 2012).

Hot-chili is one of the promising vegetable crops for Thailand and progressive growers prefer transplanting commercial seedlings into the field rather than sowing seed directly (Senadee, 2011). Therefore, seed priming technology can play an important role in enhancing the quality of hot-chili seedlings, leading to successful hot-chili production in Thailand. Unfortunately, study on the effect of drying rates on seed quality after priming of Thai hot-chili seeds has been

very limited and only two drying rates (rapid versus slow drying) have been reported in the literature by Bruggink et al. (1999). To find the optimum drying rate in the seed priming process for Thai hot-chili seed, we primed the seeds using various slow-drying rates compared to the conventional rapid drying and a control (no priming). The effects of these drying treatments with different rates on seed quality were analyzed based on germination and field emergence and vigor tests (standard germination, field emergence and the controlled deterioration (CD) tests) and headspace ethanol assay. The CD test was reported by Basak et al. (2006) as an effective method to determine seed vigor for pepper (hot-chili). The emission of headspace ethanol was also assayed to investigate the vigor of primed seeds as an effect of post-priming drying rates treatments because it has been reported that deteriorated seeds emit ethanol from the dysfunctional mitochondria through anaerobic respiration (Kodde et al., 2012) and mitochondrial degradation is the main cause of seed deterioration, leading to the loss of seed vigor (Chhabra et al., 2019). The findings from the current study should provide useful information for improving the drying method as the last step of the seed priming process for Thai hot-chili seeds.

Materials and Methods

Seed material

Commercial hybrid hot-chili seed cv. Maeping from the Known-You Seed Co., Ltd., Thailand was used in this experiment. Seeds were disinfected by soaking in 0.6% w/v sodium hypochlorite solution for 10 min, followed by washing in tap water for 10 min before they were air-dried (approx. 35–40% relative humidity (RH)) until the moisture content was reduced to 7% fresh weight (FW). Thereafter, the seeds were kept in sealed aluminum foil bags and stored at 5°C until they were used in the experiment.

Priming treatment

All hot-chili seeds except for the control treatment were primed using the best priming treatment for hot-chili seeds obtained from the preliminary study (data not shown). Seeds were soaked in 2% w/v potassium nitrate (KNO₃) solution for 72 hr at 20°C in the dark. The ratio of seed weight-to-KNO₃ solution volume was 1:10 g/mL. After soaking, the seeds were washed with distilled water and subjected to different post-priming drying treatments.

Post-priming drying treatments

Rapid drying

Seeds from above priming treatment were dried in a sealed chamber (using an internal fan for air circulation) containing a saturated calcium chloride salt (CaCl_2) solution to maintain 35% RH at 20°C (McDonald, 2007) for 72 hr.

Slow drying

There were six slow drying (SD) treatments with different drying rates. Seeds from the above priming treatment were placed in a sealed chamber (using an internal fan for air circulation) containing a saturated sodium chloride (NaCl) solution to dry the seeds using 75% RH at 20°C (McDonald, 2007) for 12 hr, 24 hr, 36 hr, 48 hr, 60 hr or 72 hr followed by the rapid drying (RD) treatment as described above. Thereafter, these slow-drying treatments were designated as SD12, SD24, SD36, SD48, SD60 and SD72, respectively.

Double slow drying

Seeds from the above priming treatment were placed in the first sealed chamber (using an internal fan for air circulation) containing saturated NaCl solution to dry the seeds at 75% RH and 20°C for 48 hr before placing them in the second sealed chamber containing saturated magnesium chloride (MgCl_2) solution to dry the seeds at 50% RH and 20°C (McDonald, 2007) for 48 hr followed by the RD treatment, as described above. Thereafter, this drying treatment was designated as DSD.

After the post-priming drying treatments, all primed hot-chili seeds as well as that of the unprimed (control) seeds were divided into two groups. Seeds from the first group were packed in aluminum-foil bags and stored in a refrigerator at 5°C before the seed quality was tested. Seeds from the second group were subjected to the CD test. The CD test was conducted according to the method described by Basak et al. (2006) with slight modifications. The seed moisture was raised to 22% FW by placing 10 g of seed with a known moisture content in a plastic box and adding 2 mL of water. The seed was allowed to imbibe water until the required seed weight was achieved that was equivalent to a seed moisture content of 22% (International Seed Testing Association, 2017). Then, they were packed in aluminum foil bags and kept at 5°C for 48 hr. Then, the packets were placed in a water bath at 45°C for 24 hr. Thereafter, the seeds were dried back to the original seed-moisture content and packed in aluminum-foil bags and stored in a refrigerator at 5°C for further seed-quality testing.

Seed-moisture content test

During the priming and post-priming drying period, seed samples were taken at intervals of 12 hr for seed moisture content (SMC) testing. The SMC was determined using the low-temperature constant method according to the International Rules for Seed Testing (2017) (International Seed Testing Association, 2017). Four replications of 2 g hot-chili seeds were dried in a hot-air oven at 103°C for 18 hr and then kept in a desiccation chamber for 30 min. The seed moisture content was calculated and expressed as a percentage of the seed FW.

Seed germination test

A seed sample of each treatment was randomly taken before and after the seed-priming process and a subsequent CD test. The seed germination test was conducted according to the International Rules for Seed Testing (2017) (International Seed Testing Association, 2017). Four replications of 100 seeds each for each treatment were germinated on the top of two layers of Whatman No. 1 filter paper moistened with 5 mL distilled water and placed inside Petri dishes (90 mm diameter). The Petri dishes were kept in a dark room at 25°C. The normal seedling number was determined daily for 14 d. The germination rate was assessed using the mean germination time calculated using a seed germination program (Joosen et al., 2010) and the number of normal seedlings was used in the calculation instead of using the number of emerged radicles.

Field emergence test

The field emergence test was conducted in a greenhouse according to the International Rules for Seed Testing (2017) (International Seed Testing Association, 2017) with a slight modification. Four replications of 100 seeds each for each treatment were germinated using sphagnum peat moss as the seedling medium. For each replication, seeds were sown in a 200-hole seedling tray and placed inside a greenhouse with 50% shade. The seedling emergence number was determined daily for 14 d. The emergence rate was assessed using the mean emergence time (MET) value calculated using the seed germination program (Joosen et al., 2010).

Headspace ethanol assay

The ethanol production assay was conducted using the method described by Kodde et al. (2012) with slight modifications. Two grams of seeds from each treatment were placed in a 20 mL glass vial. There were five replicates per treatment. Seventy μL of distilled water were added into the vial to raise the desired seed moisture content from 7% FW to 30% FW. The vials were sealed immediately after the water had been added and incubated at 25°C for 24 hr, followed by incubating in the hot-air oven at 55°C for 24 hr. The ethanol content in the headspace of the vial was measured using a modified breath analyzer (Alcotest 6810 Dräger Safety AG & Co. KGaA, Lübeck, Germany).

Statistical analysis

All data were subjected to analysis of variance (ANOVA) in which germination and field emergence data were transformed using the arc-sin method prior to the ANOVA analysis; untransformed values were shown in figures to facilitate comparison. The Duncan's new multiple range test was used for mean comparisons. All tests were considered significant at $p < 0.05$.

Results

Seed-moisture content changes

The hot-chili seeds for all post-priming drying treatments were subjected to a common priming protocol by soaking in 2% KNO_3 for 72 hr. During the soaking period, the SMC of all treatments increased rapidly from 6% FW to 42% FW

within 24 hr, after which began to stabilize for the rest of the soaking period (Fig. 1A). During the dehydration period, the SMC levels of primed seeds decreased at different rates depending on the post-priming drying treatments. The SMC of primed seeds subjected to RD treatment decreased rapidly to below 20% FW after approximately 30 hr and reached a final MC at 7% FW within 60 hr. The SMC of primed seeds subjected to SD treatments decreased more slowly than for RD treatment. They decreased to below 20% FW at different times (36–60 hr) depending on their-drying times at 75% RH. The longer the drying time, the later the SMC decreased below 20% FW. However, after the common RD treatment, their times to reach the final MC were close to each other except for SD72, whose SMC-loss characteristic was similar to that of DSD and both had the slowest SMC reduction rates (Fig. 1B).

Germination performance

The results showed that all SD and DSD treatments significantly increased the germination percentage (GP) of primed seeds compared to the control, while the RD treatment did not. Among the post-priming drying treatments, there were no significant differences in the effects of all SD treatments on the GP of primed seeds nor from that of DSD, while all SD treatments except for SD24, SD60 and DSD had significantly higher GP levels than for the RD treatment (Fig. 2A). However, the effect of post-priming drying treatments on the germination rate of primed seeds was more pronounced. The mean germination time (MGT) of primed seed for all post-priming drying treatments significantly decreased compared to the control. Among the post-priming drying treatments, the germination rate increased significantly as the drying rate

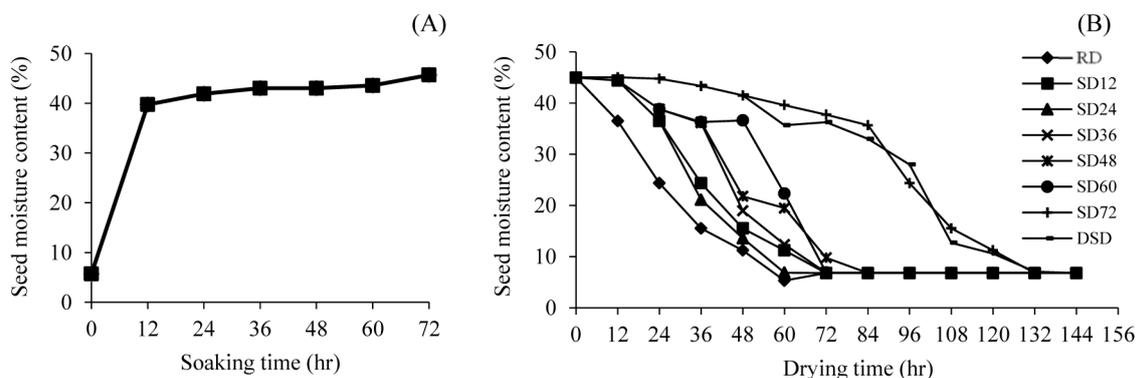


Fig. 1 Changes in seed moisture content of Thai hot-chili seed cv. Maeping: (A) during soaking in 2% W/V KNO_3 solution at 20°C for 72 hr; (B) during post-priming drying using different drying rates (RD = rapid drying; SD12, SD24, SD36, SD48, SD60, SD72 = slow drying with drying times of 12 hr, 24 hr, 36 hr, 48 hr, 60 hr, 72 hr, respectively, followed by RD; DSD = double slow drying)

decreased, with the greatest germination rate being for primed seeds subjected to the DSD treatment that produced the lowest drying rate (Fig. 2B).

Field-emergence performance

The RD treatment did not improve the field emergence (FE) of primed hot-chili seeds under greenhouse conditions. The SD treatments with drying times shorter than 72 hr also failed to improve the FE of primed seeds in the greenhouse. There were only two post-priming drying treatments that could increase the FE of primed seeds under greenhouse conditions, namely, SD72 and DSD (Fig. 3A). The FE rate results were consistent with the results from the laboratory germination test. All the post-priming drying treatments significantly hastened the FE rate and reduced the MET of the primed seeds under greenhouse conditions. The slower the drying rate, the greater the FE rate of the primed seeds. The DSD treatment produced the greatest FE rate, followed by SD72 (Fig. 3B).

Germination performance after controlled deterioration testing

The results revealed that after the subsequent CD test, the primed seeds from all post-priming drying treatments no longer had greater GP values than the control. In contrast, the GP of primed seeds after CD testing decreased as the drying rate decreased. The GP of the RD treatment remained as high as that of the control treatment, while there was a significant reduction in GP when the drying time at 75% RH for the SD treatments was more than 36 hr; the lowest GP was for primed seed subjected to the DSD treatment and they had the slowest drying rate (Fig. 4A). However, despite the loss of superior germination after the CD test, the primed seeds from all post-priming drying treatments still had a greater germination rate than the control seeds, except for the DSD treatment. Among the post-priming drying treatments, the RD treatment had the greatest germination rate, while the DSD treatment had the lowest (Fig. 4B).

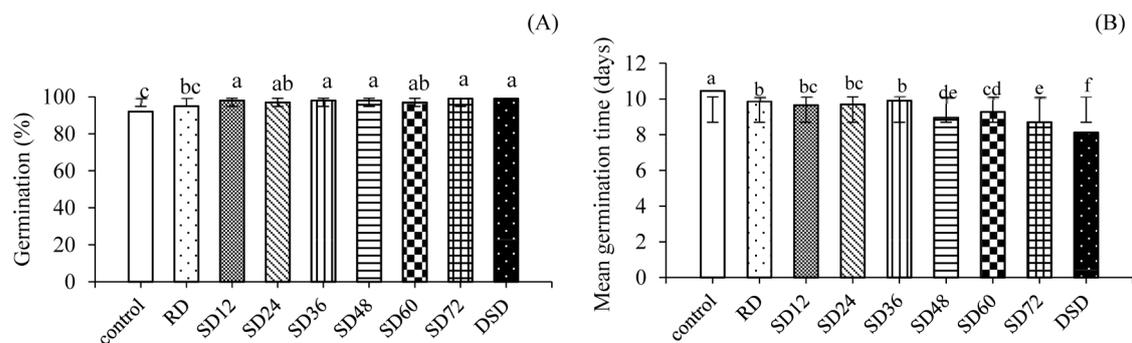


Fig. 2 (A) germination percentage and (B) mean germination time of Thai hot-chili seed cv. Maeping primed in 2% W/V KNO_3 solution at 20°C for 72 hr, followed by drying treatments with different rates (RD = rapid drying; SD12, SD24, SD36, SD48, SD60, SD72 = slow drying with drying times of 12 hr, 24 hr, 36 hr, 48 hr, 60 hr, 72 hr, respectively followed by RD; DSD = double slow drying); error bars indicate \pm SD

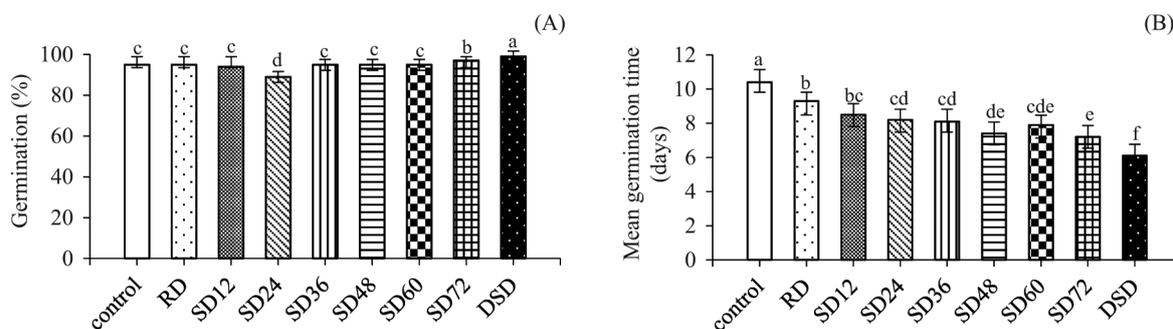


Fig. 3 (A) field emergence percentage; (B) mean emergence time in greenhouse test of Thai hot-chili seed cv. Maeping primed in 2% W/V KNO_3 solution at 20°C for 72 hr, followed by drying treatments with different rates (RD = rapid drying; SD12, SD24, SD36, SD48, SD60, SD72 = slow drying with drying times of 12 hr, 24 hr, 36 hr, 48 hr, 60 hr, 72 hr, respectively followed by RD; DSD = double slow drying); error bars indicate \pm SD

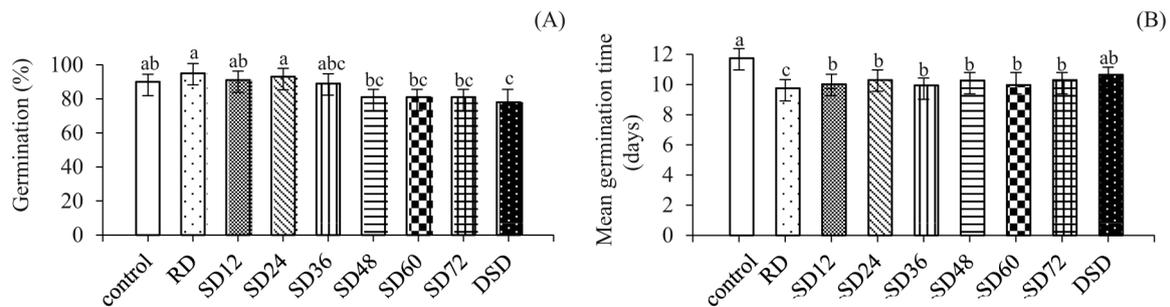


Fig. 4 (A) germination percentage and (B) mean germination time after controlled deterioration test of Thai hot-chili seed cv. Maeping primed in 2% W/V KNO_3 solution at 20°C for 72 hr, followed by drying treatment with different-rates (RD = rapid drying; SD12, SD24, SD36, SD48, SD60, SD72 = slow drying with drying times of 12 hr, 24 hr, 36 hr, 48 hr, 60 hr, 72 hr, respectively, followed by RD; DSD = double slow drying); error bars indicate \pm SD

Field-emergence performance after controlled deterioration testing

After the subsequent CD test, the FE of primed seeds from all the post-priming drying treatments decreased significantly compared to the control seed. The slower the drying rate, the higher the FE reduction after the CD test. The DSD treatment had the slowest drying rate and hence, had the lowest FE. Similar to the laboratory results, the primed seeds from all post-priming drying treatments were still able to maintain a faster FE rate in terms of MET than that of the control seeds after the CD test (Fig. 5A). However, among the post-priming drying treatments, the FE rate decreased significantly when the drying rate decreased (the drying times at 75% RH increased). Hence, the fastest FE rate after the CD test was for the RD treatment and the slowest FE rate was in the DSD treatments (Fig. 5B).

Headspace ethanol production

The headspace ethanol production during seed imbibition had a positive correlation with the level of seed deterioration and was used to detect the level of seed vigor. This experiment revealed that primed hot-chili seeds from all post-priming drying treatments had significantly lower headspace ethanol production than for control seeds. The significant differences in headspace ethanol production among post-priming drying treatments were found both before and after the CD test. The slower the drying rate, the greater the headspace ethanol production: Prior to the CD test, the SD treatments with 72 hr drying time at 75% RH and DSD treatment had the highest headspace ethanol production among the post-priming drying treatments (Fig. 6A). After the CD test, the differences in headspace ethanol production among post-priming drying treatments were more pronounced. The RD and SD treatments

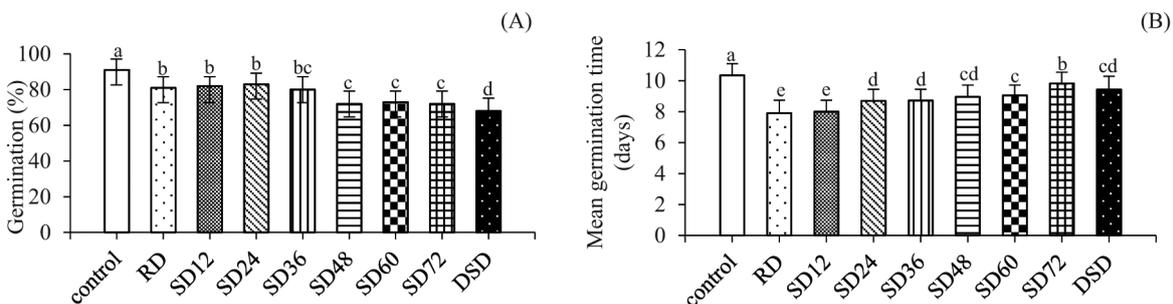


Fig. 5 (A) field emergence percentage and (B) mean emergence time after controlled deterioration test of Thai hot-chili seed cv. Maeping primed in 2% W/V KNO_3 solution at 20°C for 72 hr, followed by drying treatments with different rates (RD = rapid drying; SD12, SD24, SD36, SD48, SD60, SD72 = slow drying with drying times of 12 hr, 24 hr, 36 hr, 48 hr, 60 hr, 72 hr, respectively, followed by RD; DSD = double slow drying); error bars indicate \pm SD

with drying times at 75% RH and not more than 24 hr had significantly the lowest headspace ethanol production, followed by the SD treatments with drying times at 75% RH for 36–72 hr, with the DSD treatment having the significantly highest headspace ethanol production among the post-priming drying treatments (Fig. 6B).

Discussion

The moisture loss results during the dehydration period revealed that different post-priming drying treatments had different drying rates. RD had the most rapid drying rates, while the DSD treatment had the slowest. The drying rates of the SD treatments varied with the drying time at 75% RH. The longer the drying time, the lower the drying rate. Notably, the SD treatment with a 72 hr drying time had a similar SMC reduction to the DSD treatment, indicating that both treatments should have an equal drying rate.

It was clear in this study that the primed hot-chili seeds for all post-priming drying treatments had superior quality compared to the control (unprimed) seeds in terms of germination capacity and germination rate. After priming, the primed seeds had reached a more advanced stage in the germination process and so there were greater and more rapid germination rates than for the unprimed seeds when they were rehydrated. This explained why the primed hot-chili seeds cv.

Maeping for all post-priming drying treatments in the current study had greater and rapid germination rates than for the control (unprimed) seed. There were differences in germination improvement due to the effects of the post-priming drying treatments. The DSD, the lowest drying-rate treatment, clearly had the best germination performance for both the laboratory and greenhouse conditions. The outperformance by the SD treatments over the RD treatment varied with the formers' drying rates. Although, all six SD treatments had greater GP values than for the RD treatment, their germination rates did not outperform RD unless the drying time at 75% RH exceeded 36 h. This result indicated the critical role of the drying rate on the efficiency of seed priming to improve the quality of hot-chili seeds. The slower the drying rate, the more the SD treatment outperformed the RD and control treatments.

The results of the SMC changes during the water imbibition and post-priming drying periods (Figs. 1A and 1B) showed that at the end of phase II and in the early phase of the post-priming drying treatments, the SMC in each post-priming drying treatment remained at a high level and gradually decreased at a different drying rate depending on the post-priming drying treatment. Therefore, the pregerminative metabolism that occurred during phase II of water imbibition could possibly extend to some extent into the early phase of the post-priming drying treatments before the SMC became too low. The slower the drying rate, the longer the pregerminative

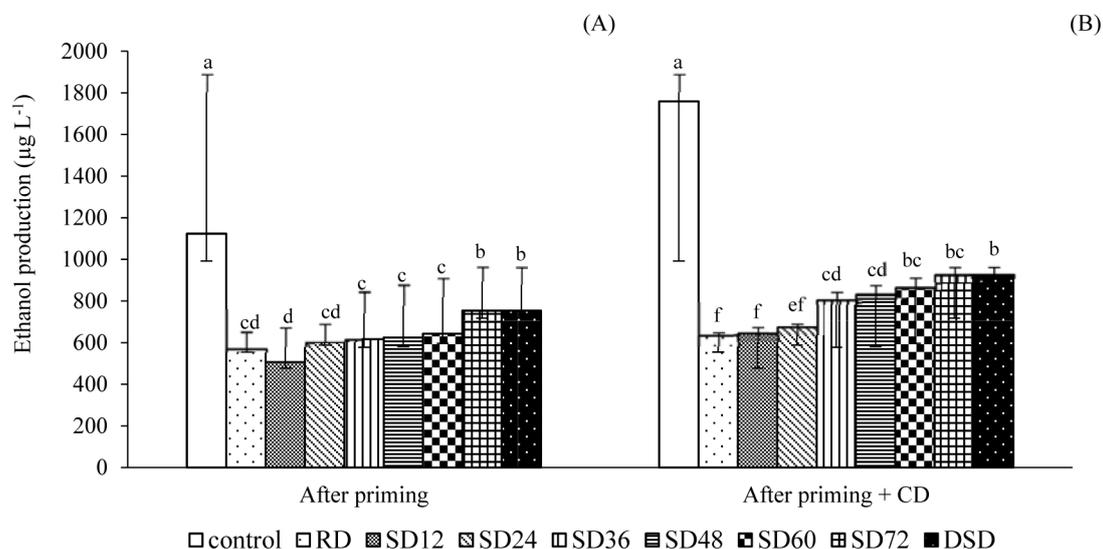


Fig. 6 Headspace ethanol production ($\mu\text{g/L}$) of Thai hot-chili seed cv. Maeping primed in 2% W/V KNO_3 solution at 20°C for 72 hr, followed by different drying rates (RD = rapid drying; SD12, SD24, SD36, SD48, SD60, SD72 = slow drying with drying times of 12 hr, 24 hr, 36 hr, 48 hr, 60 hr, 72 hr, respectively, followed by RD; DSD = double slow drying): (A) after priming; (B) after controlled deterioration treatment after priming; error bars indicate \pm SD

metabolism extended. Hence, in this study, the DSD treatment had the longest pregerminative metabolism time followed by the SD treatments, with their pregerminative metabolism time increasing as the drying times at 75% RH increased, while the RD treatment had the shortest. The difference in the pregerminative-metabolism times among the post-priming drying treatments could explain the different efficiencies of germination improvement found in this study. The above-mentioned results demonstrated that seed priming for all post-priming drying treatments not only improved the germination capacity of the primed hot-chili seeds but also their vigor regarding the germination rate in terms of MGT and the emergence rate in terms of MET. However, seed vigor is not a single trait and is composed of several seed attributes involved in the good establishment of normal seedlings under a wide range of field conditions (International Seed Testing Association, 2014). In the current study, primed hot-chili seeds had reduced germination and field emergence after the CD test. These results indicated that primed hot-chili seeds from all drying treatments were more vulnerable to hot and humid stress or the ageing conditions imposed by the CD test than the control seed. This implied that after priming, the vigor was reduced of the hot-chili seeds primed using any of the post-priming drying treatments, regarding their ability to withstand unfavorable conditions. Furthermore, there was significant variation in vigor reduction among the primed hot-chili seeds dried with different drying rates during the post-priming drying treatments. The slower the drying rate, the lower the vigor of the primed seeds after priming. The primed seed dried with DSD treatment (the slowest drying rate) had the lowest vigor, followed by that of the SD treatments with a drying time at 75% RH greater than or equal to 48 hr (a moderate drying rate) while that of the RD treatment and the SD treatments with a drying time at 75% RH less than or equal to 36 hr (the fastest drying rate) were among the group that had the highest vigor, as indicated by their field emergence and emergence rate reductions after CD testing (Fig 5).

The variation in vigor reduction of hot-chili seeds primed at different drying rates suggested that it was influenced by different levels of injurious effect imposed by the post-priming drying treatments and should be associated with a loss of desiccation tolerance (DT) by the hot-chili seeds after priming. Buitink et al. (2003) stated that, in general, seed organs, particularly the radicle part, begin to lose their DT during the seed imbibition phase of the germination process; however, they (especially orthodox seeds) can regain their DT during the period of dehydration. Even so, at a certain developmental

stage after germination, they can completely lose the ability to withstand extreme drying and become desiccation-sensitive. Thus, this ability to regain DT is strictly dependent on the developmental stage of the germinated seeds (as reviewed by Dekkers et al., 2015). During phase II of water imbibition in the seed priming process, seed metabolizes reserve food to generate energy for its germination. Hence, the excessive slow drying rate, which allowed excessive pre-germinative metabolism to occur, could have caused the seeds to lose too much soluble sugar, leading to lateral-compressive stress in the membrane and transition from the fluid phase to the gel phase (Bryant et al., 2001). This made the cell membrane of seed primed using excessive slow drying rates vulnerable to the dehydration process; when these primed seeds were subjected to the last dehydration step of rapid drying that forced the moisture to decrease rapidly, it could have led to disruption of cellular organization (Priestley, 1986). Therefore, it was likely that the post-priming drying treatments brought the primed hot-chili seeds to the germination stage so that the seeds began to lose DT and became injured during the rapid loss of SMC in the RD treatment, the last common step of all post-priming drying treatments. The extent of any injuries depended on the drying rate that varied with the advance of the germination stage. The SD72 and DSD treatments had the most advanced germination stages; hence, they had the most injury, while the RD treatment, which had the least advanced germination stage, caused the least injury to the primed hot-chili seeds.

Mitochondrial degradation is one indication of seed deterioration and loss of seed vigor. The ethanol emission from seeds with dysfunctional mitochondria can be used as an indicator of seed deterioration (Kodde et al., 2012). The objective of conducting headspace ethanol assay in the current study was to evaluate the damage to mitochondria in the cells of hot-chili seeds due to the post-priming drying treatments. The results revealed that primed hot-chili seeds had less mitochondrial damage compared to control seeds, as indicated by the lower headspace ethanol production either before or after CD testing. In seed priming, mitochondrial biogenesis occurs after RNA, DNA and protein synthesis and cell repair, taking place during the imbibition period or the metabolic activity phase of seed priming (Chen and Arora, 2013). Although the hot and humid conditions during the CD test might cause damage to the cell mitochondria of primed and unprimed hot-chili seeds to some extent, the primed hot-chili seeds should have more remaining active mitochondria compared to the control seeds. This would explain why the primed hot-chili seeds had less ethanol production in the headspace ethanol assay both before and after

CD testing. In addition, there were significant differences in mitochondrial damage among the primed hot-chili seeds dried at different drying rates was both before and after CD testing. RD had the lowest headspace ethanol production, indicating the least mitochondrial damage, while SD72 and DSD had the highest headspace ethanol production, indicating the highest mitochondrial damage among the primed seeds. Therefore, the results of mitochondrial damage supported the above finding that excessive slow drying caused vigor reduction of primed hot-chili seeds more than from rapid drying.

Consistent with the results from Basak et al. (2006) and Sano et al. (2017) who successfully used CD testing to predict the longevity of pepper (hot-chili) and *Arabidopsis* seeds, respectively, the results from the current study indicated that excessive slow drying could adversely affect the longevity of primed hot-chili seeds. However, an argument was made by Groot et al. (2012) that CD testing does not imitate seed ageing in commercial practice, and it is less effective for predicting seed longevity than the method of dry seed aging using elevated partial oxygen. Hence, the detrimental effect of excessive slow drying on the longevity of primed hot-chili seeds in the current study should not yet be considered conclusive and the effect of the post-priming drying rates on the quality of primed hot-chili seeds in storage should be further studied. Furthermore, additional monitoring of the field performance of the Thai hot-chili seedlings from primed seed dried using different drying rates might be interesting to provide information on the consequential effects of post-priming drying rates on the growth and yield of hot-chili after transplanting.

The adverse effect of slow drying on the vigor of primed seed observed in the current study was consistent with Lin et al. (2005) who studied primed bitter melon, but was contradictory to a number of reports in different species: lettuce (Schwember and Bradford, 2005), celery (Coolbear et al., 1992), pepper and pansy (Bruggink et al., 1999) and tomato (Gurusinghe et al., 2002). The review by Girolamo and Barbanti (2012) considered that variation in the effect of slow drying on the quality and longevity of primed seeds may have been caused by the different responses of different seed kinds or different drying methods or both. In addition, crop varieties and seed lots could play a role in the response of primed seeds to drying treatments (Maiti et al., 2013; Ellis and Butcher, 1987). Hence, variation to some extent in the response of primed hot-chili seed to the post-priming drying treatments is possible where different varieties and seed lots are used. Nevertheless, the findings from the current study could provide a good reference for seed companies who plan to conduct priming for Thai hot-chili seeds.

In conclusion, post-priming slow drying was more effective at enhancing the initial quality of Thai hot-chili seeds cv. Maeping than conventional rapid drying. However, if the drying rate is too slow, it can adversely affect the seed vigor in terms of its tolerance to hot and humid conditions, so proper storage conditions must be considered and applied when storing primed Thai hot-chili seeds. The optimum post-priming drying treatment for primed Thai hot-chili seed from the current study were to dry the seed at 75% RH and 20°C for 12 hr, followed by conventional rapid drying involving drying the primed seed at 35% RH and 20°C for 3 d.

Conflict of Interests

The authors declare that there are no conflicts of interests.

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