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Dehydration Rate after Solid Matrix Priming Alters Seed Performance of *Shrunken-2* Corn

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***Abstract*. In a test to overcome poor seed germination and seedling vigor of sweet corn (*Zea mays* L.) seeds carrying the *shrunken-2 (sh2)* mutant endosperm, primed seeds of two *sh2* sweet corn cultivars—Crisp N'Sweet 711 (CNS-711) and How Sweet It Is (HSII)—were redried at 15, 20, 30, or 40C and 25% relative humidity after solid matrix priming (SMP). The dehydration rate was significantly lower in 'CNS-711' than 'HSII' at all temperatures. In both cultivars, the drying temperature after SMP was critical for seed performance. Primed seeds with a higher dehydration rate (dried at 30 or 40C) had better seed vigor, greater field emergence and seedling vigor, lower leachate conductivity and imbibition rate, and a higher respiration rate and glutamic acid decarboxylase activity than primed seeds redried at the lower temperatures or control seeds. Increased incidence of pathogen growth was observed on seeds dried at 15 and 20C relative to those dried at 30 or 40C, probably as a consequence of greater leakage from the seeds at a lower redrying temperatures. Lack of tolerance to dehydration at 15 and 20C was another factor adversely affecting the seeds redried at low temperature. A more rapid dehydration rate at a higher temperature after priming *sh2* sweet corn improved many of the physiological characteristics used to measure seed quality and the subsequent emergence and vigor of the seedlings under field conditions.**

In maize, the *shrunken-2 (sh2)* endosperm mutation increases endosperm sugar retention and concentration, improving postharvest storage properties and fresh eating quality (Laughnan, 1953). However, poor germination and seedling vigor is a common characteristic of *sh2* cultivars (Wann, 1980). The poor seed and seedling vigor in *sh2* sweet corn could be an interaction of several factors previously reported: deficient mobilization of reserves by the embryo (Styer and Cantliffe, 1984), potential imbibition damage (Chern and Sung, 1991; Parera and Cantliffe, 1991), reduced seed maturity at harvest (Borowski et al., 1991), and greater susceptibility to seed- and soilborne diseases (Berger and Wolf, 1974).

Seed priming is a presowing treatment used to increase germination rate and synchronize germination in many species (Bradford, 1986; Khan, 1992). Germination and emergence have generally not been improved in sweet corn seeds primed with osmotic solutions (Bennett and Waters, 1987). Solid matrix priming (SMP) is another priming technique, during which the seeds are mixed and incubated with water and a solid matrix such as calcined clay (Kubik et al., 1988) or leonardite shale (Harman and Taylor, 1988) in place of a liquid osmoticum. SMP treatments with leonardite shale as a solid matrix successfully increased the germination rate of tomato (*Lycopersicon esculentum* Mill.), onion (*Allium cepa* L.), and carrot (*Daucus carota* L.) (Taylor et al., 1988). In *sh2* sweet corn, SMP combined with sodium hypochlorite has increased germination, field emergence, and seedling vigor (Parera and Cantliffe, 1992). After priming, the seeds must be dried for storage or planting. However, conditions for redrying the seeds after priming have not been studied extensively, regardless of priming method.

Corn ears produced for seed are usually harvested at a relatively high moisture content (40% to 50%) to avoid deterioration in the field and decrease damage during harvest (Herter and Burris, 1989). Seeds are subsequently dried in hot air to 11% to 12% moisture (Seyedin et al., 1984). The temperature and dehydration rate can affect germination percentages and seedling vigor of corn seeds (Herter and Burris, 1989).

During corn seed drying, membranes and the pericarp are susceptible to damage (Wann, 1980). Cell membrane injury in soybean (*Glycine max* L.) cotyledons has been detected through leachate electrical conductivity (EC) (Schoettle and Leopold, 1984). In sweet corn hybrids carrying the *sh2* mutant endosperm, high leachate EC and imbibition rate have been negatively correlated with germination in the laboratory (Parera and Cantliffe, 1991) and emergence in the field (Waters and Blanchette, 1983). Several tests have been developed to relate damage to membranes and poor seed quality. In the first germination stage, seed respiration rate is a good indicator of corn seed quality and seedling vigor (Woodstock and Grabe, 1967). Seed deterioration has been correlated with low activity of glutamic acid decarboxylase in seeds (Linko, 1961). Low metabolic activity has been reported in seeds injured by chilling temperatures (Herner, 1986). The complex stress vigor test (CST) and the index of conductivity and stress vigor test (ICST) are, alone or combined, reliable indicators of seed vigor for *sh2* corn (Parera, 1992).

The objective of the present study was to investigate the effects of drying rate, as influenced by temperature, on seed quality after solid matrix priming on two *sh2* sweet corn cultivars. Laboratory and field tests were conducted to determine changes in seed vigor of *sh2* primed seeds redried at various temperatures.

Materials and Methods

Plant material and solid matrix priming treatment

Two cultivars of sweet corn with *sh2* mutant endosperm—'How Sweet It Is' (HSII) and 'Crisp N' Sweet 711' (CNS-711) (Crookham Seed Co., Caldwell, Idaho)—were used in this study. Before and after treatment, the seeds were stored at 15C in 45% relative humidity (RH). Seeds were not generally retained for more than 1 month after treatment.

Seeds were primed via SMP using calcined clay as the solid matrix and sodium hypochlorite. The procedures were similar to those of Parera and Cantliffe (1991) but were modified slightly to

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improve the results of SMP, especially when large quantities of seed may be primed at one time. Seeds (9 g) were mixed in a container with 27 g of calcined clay (Emathlite; Mid-Florida Mining, Lowell, Fla.) and 14 ml of a 0.1% solution (by volume) of sodium hypochlorite, incubated at 5C for 6 h, then moved to 25C for another 66 h under continuous rotation (20 rpm). The seeds were dried in a single layer in a controlled-temperature incubator to their original fresh weight (6% to 7% moisture) at 15, 20, 30, or 40C and 25% RH (vapor-pressure deficit, –13, 18, 32, and 50 mb, respectively). The dehydration rate was calculated hourly on 25 seeds and expressed as a percentage of the original fresh weight until the seeds were completely dry (HSII) or hourly for the first 6 h (CNS-711) then at each 10-h interval.

Laboratory studies

Leachate conductivity. Twenty seeds were soaked in 25 ml of distilled water at 25C. Leachate EC was measured each hour up to 6 h (Parera, 1992) by a conductivity meter (Lecto Mho-meter; Lab-Line Instruments, Melrose Park, Ill.) and expressed as $\mu mhos \cdot g^{-1}$ of seed.

Seed imbibition. Seeds (25) were soaked in 25 ml of distilled water at 25C. Imbibition was calculated at 2, 4, 8, and 16 h and expressed as percentage increase in fresh weight.

Seed respiration. Seed respiration was monitored in a differential respirometer (Gilson Medical Electronics, Middleton, Wis.). Five seeds were placed in a 15-ml vessel with 0.2 ml of 10% KOH in the center well and incubated at 25C and 85 oscillations/min in darkness. Oxygen depletion was calculated 15 min and 4, 16, and 32 h after imbibition and expressed as $\mu l\ O_2$.

Glutamic acid decarboxylase (GAD). Evolution of CO_2 was measured in a differential respirometer. In a 15-ml reaction flask, 1 g of ground seed was mixed with a solution of 2.5 ml 0.1 M glutamic acid in 0.067 M phosphate buffer at 5.8 pH (Ram and Wiesner, 1988) and incubated as previously described for seed respiration. Production of CO_2 was measured for 10 min after a stabilization period of equal duration. Results were expressed as $\mu l\ CO_2/g$ per min.

Sugar determination. Embryos (25 axes plus scutellum) were separated from the endosperm. Both seed fractions were homogenized (Virtis homogenizer; Virtis Co., Gardiner, N.Y.) with 10 ml of 80% ethanol. The homogenate was centrifuged at 20000× *g* for 10 min. The supernatant was separated and the pellet was washed with 5 ml of 80% ethanol. The supernatants were combined and recentrifuged (Chen and Burris, 1990). The ethanol was removed by forced-air evaporation at 30C. Water (5 ml) was added to the extract and filtered through a 0.2-μm pore nylon filter. The sugars were analyzed in a high-performance liquid chromatograph (BioRad Chemicals, Richmond, Calif.). The sugars were separated on a carbohydrate column (HPX-87C, Aminex, BioRad) with water as a mobile phase at a flow rate of 0.6 $ml \cdot min^{-1}$. Sugars were quantified by comparing areas under peaks of interest with those of comparable standards and expressed as $mg \cdot g^{-1}$ of fresh weight.

Germination test. Seeds (25) were placed in a 15-mm petri dish on blue blotter germination paper (Anchor Paper Co., St. Paul, Minn.) and incubated in darkness at 25C. After 7 days, germination percentage was calculated. Pathogen growth and development were visually evaluated in each seed treatment.

CST. Seeds (200) were soaked for 24 h in 250 ml of distilled water at 25C then transferred to 5C for an additional 24 h (Barla-Szabo and Dolinka, 1988). After soaking, 25 seeds were placed with the radicle pointing downward on three layers of moist, nontoxic, germination paper (Anchor Paper Co.). The paper was rolled, placed in a plastic container (21.5 × 32.5 × 5.5 cm), and incubated in the dark at 25C for 4 days. Leachate EC was measured after each soaking period. Germination percentage and an ICST, which combines EC after each soaking period and germination percentage, were calculated (Parera, 1992).

Field studies

Treatments were tested in two field trials established on 3 Dec. 1991 and 13 Apr. 1992 at the Institute of Food and Agricultural Sciences Horticultural Research Unit (Gainesville, Fla.) on an Arredondo fine sand soil (loamy, siliceous, hyperthermic Grossarenic Palenundult). Seeds were sown 4 cm deep every 30 cm in twin-row plots with 50 seeds planted per plot. The plot length was 7.6 m on beds with 1.2 m centers. The emergence rate index (ERI) (Shmueli and Goldberg, 1971) and percentage emergence were calculated for each plot. Fresh and dry weights of five seedling shoots were recorded 14 days after sowing. Each was cut at the soil level and oven-dried for 4 days at 75C.

Statistical analysis

All experiments were conducted as a randomized complete-block design with four replications. Percentage data were arcsin-transformed before analysis. The respiration, imbibition, and leachate EC experiments were each analyzed as split blocks considering time as the main block. Main effects of the treatments were partitioned using a single degree of freedom orthogonal contrast.

Results

In both cultivars, the seed moisture content increased from storage levels (6% to 7%) to 45% to 54% after priming (Fig. 1, 0 h). There were significant differences between the two cultivars when the dehydration rate after priming was calculated (Table 1). 'HSII' seeds desiccated more rapidly after priming than 'CNS-711' seeds, regardless of the drying temperature. The dehydration rate also was highest at 40C in both cultivars. In 'HSII', the dehydration rate in seeds redried at 15 or 20C did not differ (Table 1).

A significant cultivar × treatment interaction occurred when imbibition rate and leachate EC were evaluated, thus the main effects were analyzed separately (Table 2). 'CNS-711' seeds had a lower imbibition rate and leachate EC than 'HSII', regardless of the dehydration treatment. As previously reported (Parera and Cantliffe, 1991), SMP significantly reduced imbibition and seed leakage in *sh2* sweet corn seeds compared to nonprimed seeds (Table 2). When 'HSII' seeds were primed and dried at 15 or 40C, they imbibed more water compared to seeds dried at 20 or 30C. More importantly, the seeds dried at 30 or 40C produced significantly lower leachate EC than seeds from the other temperatures, regardless of cultivar. The nonprimed seeds had higher ECs than primed seeds.

Cultivar and dehydration rate did not interact significantly with respect to seed respiration. Primed and nonprimed seeds had the same respiration rate after 0.25 h of stabilization (Fig. 2); however, after 4 h of imbibition, O_2 uptake was significantly greater in primed seeds redried at 20, 30, or 40C relative to those redried at 15C or not primed. After 16 h of imbibition, seeds redried at 30C had the highest respiration rate. Oxygen uptake rates 32 h after imbibition remained higher in seeds redried at high temperatures (30 and 40C) than at 15C.

GAD activity was higher in 'CNS-711' than in 'HSII' seeds. In both cultivars, GAD activity was highest in seeds dried at 40C (Table 3).

Cultivars differed in sucrose concentration in endosperm and

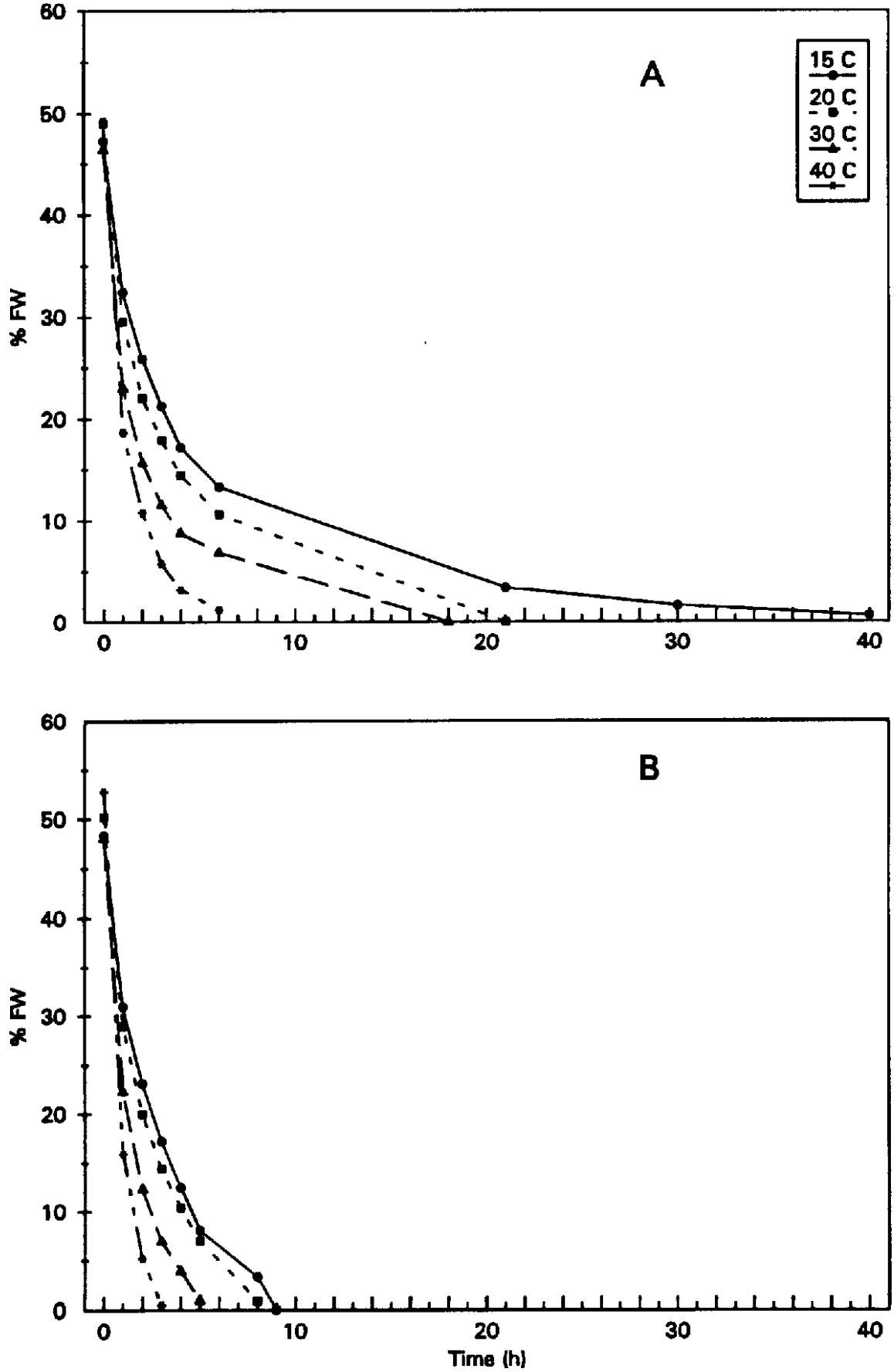

Fig. 1. Moisture content changes, calculated as percentage of the original fresh weight (6% to 7%) of 'Crisp N'Sweet 711' (**A**) and 'How Sweet It Is' (**B**) *shrunken-2* sweet corn seeds redried at different temperatures after priming.

Table 1. Dehydration rate of 'Crisp N'Sweet 711' (CNS-711) and 'How Sweet It Is' (HSII) *shrunken-2* sweet corn seeds redried at different temperatures after priming.

	Dehydration rate ($mg \cdot h^{-1}$)	
Drying temp (°C)	CNS-711	HSII
15	48	241
20	67	254
30	97	337
40	361	620
Significance	C**	Q**

**Significant at $P \leq 0.01$; Q = quadratic, C = cubic.

Table 2. Imbibition rate (based on percentage fresh weight) and leachate conductivity of solid matrix primed 'Crisp N' Sweet 711' (CNS-711) and 'How Sweet It Is' (HSII) *shrunken-2* sweet corn seeds after drying at different temperatures compared to nonprimed seeds.

Drying	Imbibition rate[z] ($mg \cdot h^{-1}$)		Conductivity[y] ($mS \cdot g^{-1}$)	
temp (°C)	CNS-711	HSII	CNS-711	HSII
15	73	91	58	128
20	64	76	74	150
30	74	74	52	59
40	71	88	53	84
Nonprimed	94	111	89	220
Contrasts				
Nonprimed vs. other	**	**	**	**
Temp	C*	Q**	C**	C**

[z]Data pooled over 16 h of imbibition.
[y]Data pooled over 6 h of imbibition.
*,**Significant at $P \leq 0.05$ or 0.01, respectively; Q = quadratic, C = cubic.

Table 3. Glutamic acid decarboxylase (GAD) activity of solid matrix primed 'Crisp N'Sweet 711' (CNS-711) and 'How Sweet It Is' (HSII) *shrunken-2* sweet corn seeds redried at different temperatures compared to nonprimed seeds.

	GAD activity ($\mu l \cdot g^{-1} \cdot min^{-1}$)	
Drying temp (°C)	CNS-711	HSII
15	170	105
20	178	84
30	183	101
40	288	136
Nonprimed	165	98
Contrasts		
Nonprimed vs. other	**	NS
Temp	Q**	Q**

NS,**Nonsignificant or significant at $P \leq 0.01$, respectively; Q = quadratic.

Table 4. Sucrose concentration in endosperm and embryo of solid matrix primed 'Crisp N'Sweet 711' (CNS-711) and 'How Sweet It Is' (HSII) *shrunken-2* sweet corn seeds redried at different temperatures compared to nonprimed seeds.

	Sucrose ($mg \cdot g^{-1}$)			
	Embryo		Endosperm	
Drying temp (°C)	CNS-711	HSII	CNS-711	HSII
15	1.7	2.2	0.5	1.0
20	1.8	2.8	0.5	1.2
30	1.7	2.3	0.4	1.7
40	1.4	2.2	0.4	0.8
Nonprimed	2.3	2.0	0.6	0.5
Contrasts				
Nonprimed vs. other	**	**	**	**
Temp	C*	C**	NS	C**

NS,*,**Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively; C = cubic.

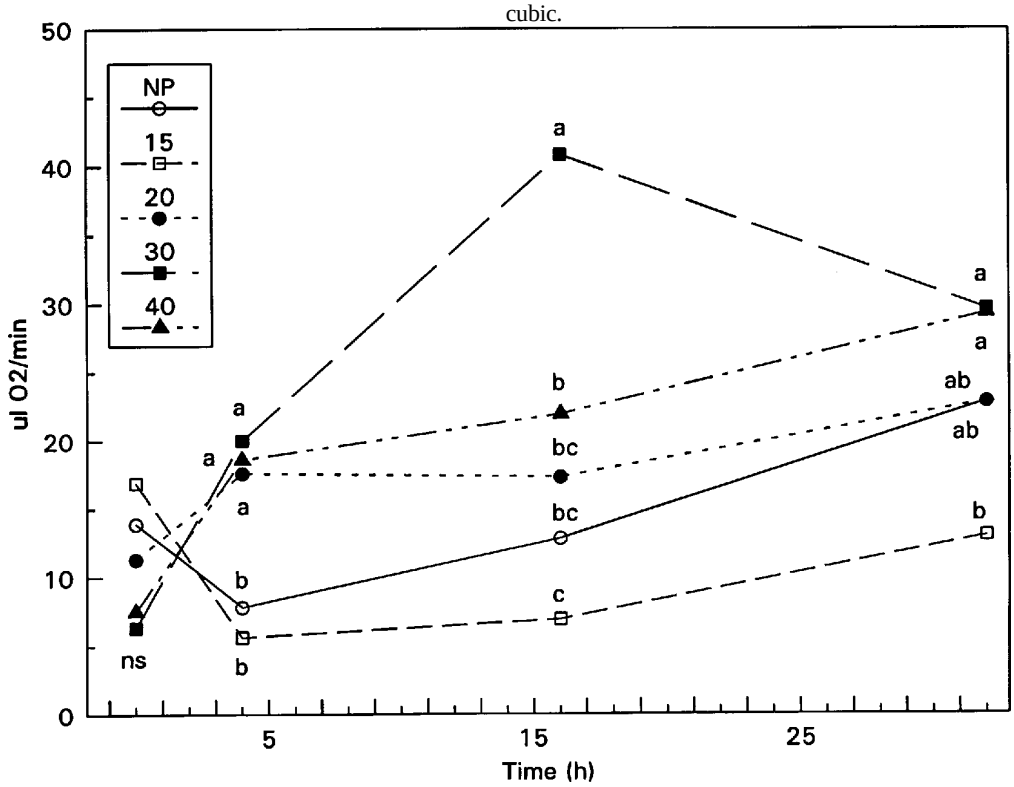

Fig. 2. Respiration rate of solid matrix primed 'Crisp N'Sweet' and How Sweet It Is' *shrunken-2* sweet corn seeds redried at various temperatures and of nonprimed seeds (data pooled for both cultivars). Values followed by the same letter are not significantly different at $P \leq 0.05$ by LSD.

embryo (Table 4) but not in raffinose, glucose, and fructose concentration (data not shown). The embryo and endosperm of 'HSII', which has a smaller and more severely shrunken seed, contained more sucrose than the 'CNS-711' counterparts at all redrying temperatures tested. Amounts of sucrose in the endosperm and embryo of primed 'CNS-711' seeds were significantly lower than those in the same tissue in nonprimed seeds. The reverse was evident in primed 'HSII' seeds, in which significantly more sucrose was present in the embryo and endosperm of primed than in nonprimed seeds, regardless of the drying temperature.

When germination and seed vigor were evaluated, the cultivars also had different responses to the redrying temperatures (Table 5). Final germination and seed vigor were evaluated by the ICST and germination percentage test after the CST, and were higher in 'CNS-711' than 'HSII', regardless of the seed treatment. When 'CNS-711' seeds were dried at the lower temperatures (15 and 20C), they had lower final laboratory germination, percentage of germination in the CST, and lower ICST values than seeds redried at the higher temperatures (30 or 40C) or those not primed. The 'HSII' seeds dried at 15C had the lowest germination in both tests. Primed 'HSII' seeds had the same percentage germination in the laboratory germination test as nonprimed seeds. Seeds dried at 40C had the highest germination percentage after the ICST.

In the laboratory germination test and CST, primed seeds dried at 15 or 20C and nonprimed seeds exhibited more pathogen growth than seeds from the 30 or 40C drying treatment (data not shown). Little or no root development was also observed in many seeds redried at 15 or 20C.

Under severe field low-temperature conditions during December, the 'CNS-711' primed seeds redried at 15 or 20C had significantly lower emergence rates and final emergence percentages than those redried at higher temperatures or those receiving no priming (data not shown). Seeds redried at 30C germinated significantly faster (higher ERI) compared to the other primed or nonprimed seeds.

In Spring 1992, 'CNS-711' emerged faster and had a higher emergence percentage and seedling fresh and dry weights than 'HSII' (Table 6). The 'CNS-711' primed seeds redried at 30C had higher ERI and seedling vigor (higher fresh and dry weights) than nonprimed seeds or the rest of the seeds from the other treatments. Seeds redried at 15C had lower ERI and emergence percentage relative to seeds from the rest of the temperatures. Primed 'HSII' seeds redried at 20, 30, or 40C had a higher ERI and greater final germination percentage than seeds dried at 15C or nonprimed seeds. Also, the primed seeds produced more vigorous (higher fresh and dry weights) seedlings than nonprimed seeds.

Discussion

Our previous results demonstrated that SMP combined with sodium hypochlorite is a valid alternative to using fungicides to increase seed performance of *sh2* sweet corn cultivars (Parera and

Table 5. Laboratory germination (LGE), germination percentage after the complex stress vigor test (CST), and index of conductivity and stress vigor test (ICST) of 'Crisp N'Sweet' (CNS-711) and 'How Sweet It Is' (HSII) *shrunken-2* sweet corn seeds redried at different temperatures compared to nonprimed seeds.

	Germination and vigor test					
	LGE (%)		CST (%)		ICST	
Drying temp (°C)	CNS-711	HSII	CNS-711	HSII	CNS-711	HSII
15	75	56	23	13	0.39	0.11
20	85	71	70	53	1.23	0.49
30	97	85	87	48	1.47	0.44
40	94	73	88	63	1.45	0.71
Nonprimed	96	64	87	37	1.50	0.28
Contrasts						
Nonprimed vs. other	**	NS	**	NS	**	NS
Temp	Q**	Q**	C**	C**	C**	C**

NS,**Nonsignificant or significant at $P \leq 0.01$, respectively; Q = quadratic, C = cubic.

Table 6. Emergence rate index (ERI), emergence (E) percentage, and seedling fresh weight (FW) and dry weight (DW) of 'Crisp N'Sweet' (CNS-711) and 'How Sweet It Is' (HSII) *shrunken-2* sweet corn seeds redried at different temperatures compared to nonprimed seeds. Field trial was sown 13 Apr. 1992, in Gainesville, Fla.

	Cultivar							
	CNS-711				HSII			
Drying temp (°C)	ERI	E (%)	FW[z] (g)	DW[z] (g)	ERI	E (%)	FW (g)	DW (g)
15	45	70	3.48	0.47	27	32	1.34	0.20
20	83	81	3.23	0.47	41	50	1.62	0.23
30	103	92	6.76	0.86	42	50	1.92	0.27
40	81	81	4.02	0.55	49	53	1.95	0.27
Nonprimed	70	78	3.03	0.44	16	20	0.99	0.15
Contrasts								
Nonprimed vs. other	**	NS	**	**	**	**	**	**
Temp	C*	Q*	C**	C**	C**	Q**	Q**	Q**

[z]Average of five plants 14 days after sowing.
NS,*,**Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively; Q = quadratic, C = cubic.

Cantliffe, 1992). The redrying temperature used in our previous reports was 25C. Primed seeds had less leakage, reduced imbibition rate, a higher respiration rate and GAD activity, more seed vigor and field emergence, and greater seedling vigor. However, the present work demonstrated that the advantages of SMP can be seriously reversed by the temperature of seed dehydration after priming. The potentially adverse effect of dehydration after priming was more severe in 'HSII', possibly due to its lower overall seed vigor.

Nass and Crane (1970) concluded that, in addition to pericarp thickness and permeability, the characteristics of the endosperm (hydrophilic compounds) were factors affecting dehydration rate in corn. The *sh2* mutation results in an elevated concentration of sucrose and a reduced amount of water-soluble polysaccharides and starch in the kernel (Creech, 1956). In the present study, the concentration of sucrose per unit of weight of 'HSII' kernels was almost twice that in 'CNS-711'. The former cultivar also dried significantly faster after priming at each temperature studied (Fig. 1b).

Good membrane integrity has been associated with good seed vigor in many species. Laboratory tests to evaluate seed vigor in garden pea (*Pisum sativum* L.), corn, and soybean have been based on seed membrane leakage (Association of Official Seed Analysts, 1983). Consistent with this relationship was the observed effect of SMP on reducing the leakage and imbibition rates of *sh2* sweet corn seeds.

Chilling injury in seeds has been observed during the initial stages of imbibition (Pollock and Toole, 1966) or after 2 days of imbibition (Christiansen, 1967). According to Hoekstra (1983), the loss of membrane integrity is the primary cause of imbibitional chilling injury resulting in elevated leakage of metabolites. Dehydration at low temperatures might result in disruption of membrane integrity. High levels of seed leakage can also contribute to increased fungal infection and development (Schroth and Cook, 1964). In the present study, more pathogen growth was observed around primed seeds dried at 15 or 20C than at 30 or 40C, even though NaOCl was used in the priming process.

The embryo has been reported to be the predominant source of leached electrolytes in aging corn seeds (Bruggink et al., 1991). Seed germination mechanisms are initiated during priming, but radicle protrusion is restricted by controlled water uptake and redrying before growth actually begins. When seeds were dried at the lower temperatures, the arrest of germination may not have been rapid enough and the embryos continued to grow. The embryo might then pass the threshold of desiccation tolerance (i.e., irreversible cell division), thus injuring membranes in the embryo beyond the point of recovery. The radicle tip is the first tissue injured by desiccation of imbibed seeds (Koster and Leopold, 1988) or by chilling temperatures (Harrington and Kihara, 1959). Damage to the radicle tips was observed in both cultivars when the seeds were redried at 15 or 20C.

The metabolic activity of the seeds in this experiment (seed respiration and GAD activity) was significantly modified by the redrying temperature. The high respiration rate observed in seeds redried rapidly (at 30 and 40C) compared to those redried more slowly (at 15 and 20C) or to nonprimed seeds may possibly reflect greater substrate supplies available to embryos of seeds showing low leakage during imbibition. A high negative correlation between sugar concentration of the leakage solution and germination in *sh2* sweet corn has been reported (Parera and Cantliffe, 1991). Chilling temperature damaged the cytochrome pathway, thus reducing respiration rates in soybean axes (Leopold and Musgrave, 1979). The low respiration rate observed in seeds redried at 15C could also be associated with a slow down of or damage to enzymatic systems involved in respiration.

The results presented here support a critical role for the membrane system in optimal germination of *sh2* corn seeds. Our data also demonstrated that the benefits to germination conferred by SMP can be seriously modified by the redrying temperature after priming. Lack of tolerance to dehydration, increased fungal attack, and injury to the embryo are potential factors reducing germination and seedling growth of primed seeds dried at low temperatures. A rapid dehydration rate after priming *sh2* sweet corn improved many of the physiological characteristics used to measure seed quality and the subsequent emergence and vigor of the seedlings under field conditions.

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