J. Amer. Soc. Hort. Sci. 112(3):427–432. 1987.

Osmotic Priming of Tomato Seeds: Effects on Germination, Field Emergence, Seedling Growth, and Fruit Yield

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Additional index words. *Lycopersicon esculentum*, osmotic conditioning, seed priming, polyethylene glycol, potassium nitrate, seedling emergence

Abstract. **Osmotic priming of seed was evaluated as a means of improving stand establishment, early seedling growth, and yield of processing tomatoes (*Lycopersicon esculentum* Mill. cvs. UC204 and 6203). Seeds were primed in aerated solutions of 3% KNO_3 (w/v) or of polyethylene glycol 8000 (PEG) of equivalent osmotic potential (−1.25 MPa; 314 $g \cdot kg^{-1}$ of water) at 20°C for 7 days, rinsed, and dried in forced air at 30°. Under laboratory conditions, seeds primed in either osmoticum germinated more rapidly than untreated seeds at 20° and 30°. At 10°, the PEG treatment was of little benefit for either variety, while the KNO_3 treatment still reduced the time to 50% germination to 60% to 80% of the control value. Priming did not affect the final germination percentage. Seedling emergence in the field was evaluated in March and April planting dates. In both trials, seedlings from primed seeds emerged earlier and more uniformly than seedlings from untreated seeds. Seedlings from primed seeds maintained greater mean plant dry weights, leaf areas, and ground cover percentages than untreated seedlings throughout the preflowering period. This advantage was due entirely to early emergence rather than to an increased relative growth rate. The early growth advantage from seed priming did not improve earliness of maturity, total yield, or soluble solids content of fruit.**

Stand establishment is a critical stage of crop growth, particularly for direct-seeded tomato. Osmotic conditioning, or priming, of seeds has been shown to result in more rapid and uniform germination at suboptimal temperatures in laboratory and greenhouse trials (4). Several studies have found that priming tomato seeds in solutions of potassium salts reduced the time to 50% germination, particularly at low temperatures (9, 10, 13, 17, 20). Heydecker et al. (15) and Rumpel and Szudyga (23) demonstrated the effectiveness of the inert osmoticum PEG 6000 in treatments for improving the germination rate and uniformity of tomato seeds. Field trials in which the effects of seed priming on tomato seedling emergence have been tested indicate that seed priming can accelerate emergence (9, 13, 23, 30).

A major question remaining is whether early emergence due to the seed treatments will be followed by differences in growth rate, maturity date, total yield, or fruit quality. As a result of early emergence after priming, increased mean plant weights have been reported for carrot (*Daucus carota* L.), celery (*Apium graveolens* L.), onion (*Allium cepa* L.), and leek (*Allium porrum* L.) (5, 7). Early maturity and increased yields due to rapid emergence from primed seeds have been noted in onion (19) and carrot (28), crops in which the vegetative organs are harvested. Early maturity has been observed in tomato crops established by fluid drilling of pregerminated (12, 29) or osmoconditioned (30) seeds and recently has been reported for primed seeds planted by conventional techniques (3). In early work on seed hardening, Henckel (14) claimed that the pretreatments enhanced photosynthetic activity per unit leaf area, leading to increased dry matter production and yield in several crops, including tomato. Increased leaf area duration due to early emergence might enhance yield or fruit solids content by increasing the amount of light intercepted by the canopy throughout the season (25). Mart'yanova et al. (21) reported that wetting and drying of tomato seed prior to planting more than doubled total fruit yield, primarily due to an increased average fruit weight. To investigate these possibilities, we determined seedling emergence, relative growth rate, canopy development, and fruit yield and quality as influenced by osmotic priming of tomato seeds.

Materials and Methods

Seed material. Tomato seeds of 'UC204' and '6203' were obtained from the Campbell Institute for Research and Technology, El Macero, Calif., and A.L. Castle, Inc., Morgan Hill, Calif., respectively. Seeds of each cultivar were primed in aerated solutions (10 $ml \cdot g^{-1}$ of seed) of 3% KNO_3 (w/v) or of PEG 8000 of equivalent osmotic potential (−1.25 MPa; 314 $g \cdot kg^{-1}$ of water) under fluorescent light at 20°C for 7 days. The moisture content of the seed batches was determined at the end of the priming treatment using the oven method (2 hr at 135°). Moisture content of the 'UC204' seeds primed in KNO_3 solution averaged 65.4% ± 1.5% (dry-weight basis), whereas the corresponding value for '6203' seeds was 70.7% ± 1.4%. A small proportion of seeds (<5%) germinated during the priming treatment in the KNO_3 solution and were removed from the petri dishes prior to the germination tests. Seeds primed in PEG solution attained 60.1% ± 1.3% and 62.4% ± 1.8% moisture content for 'UC204' and '6203', respectively. Solute uptake by the seeds in KNO_3 solution apparently accounted for the differences in final moisture content. The remaining primed seeds were rinsed thoroughly in distilled water and dried in a rotating forced-air dryer at 30° to a moisture content in the range of 6% to 7%. Controls were the untreated dry seed (6% moisture content) of each cultivar. The seeds then were stored at 6° and 30% RH until needed.

Laboratory germination. A germination test was performed 1 month after priming to assess the effects of the priming treatments. Seeds were placed on germination blotters in covered 9-cm petri dishes and wetted with 4.8 ml of distilled water. Each dish contained 100 seeds, and there were four replicate dishes

Received for publication 14 July 1986. This research was supported by funds from AES/USDA Regional Research Project W-168 and grants from the California Tomato Research Institute, Inc. The technical assistance of Z. Stan Skibinski and Stacy Lee in some of these experiments is gratefully acknowledged. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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per treatment. Dishes were put into polystyrene boxes lined with moist paper towel. The boxes were covered with black polyethylene and placed in incubators at 10°, 20°, and 30°C (±1°). Radicle protrusion to 4 mm was scored as germination. Counts of the number of seeds germinated were made at 8-hr intervals until no further germination was observed. The mean time to germination (T_{50}) was calculated from the equation:

$$T_{50} = \frac{\sum T_i N_i}{\sum N_i};$$

where N_i is the number of newly germinated seeds at time T_i.

Field studies. Field plantings of primed and control seeds of each variety were established in a Yolo loam soil (Typic Xerorthent) at the Univ. of California, Davis, on two planting dates: 10 Mar. and 11 Apr. 1984. The same seed lots also were planted in sterilized potting soil in flats in a lathhouse where the soil temperature was allowed to fluctuate with the ambient conditions. Both field experiments were arranged in a split-plot design, with varieties as the main plots and the seed treatments as subplots. There were five and six replicates for the March and April plantings, respectively. Seeds were planted 3 cm deep with a planter previously calibrated to drop a known number of seeds per unit distance of row. These values were used to estimate the percentage of seeds planted that actually emerged. The individual plots were single 20-m rows on 1.5-m beds. Soil thermocouples were placed at seed depth to monitor soil temperatures during emergence. Daily emergence counts were taken from a 5-m section of each plot, until no further emergence occurred. Seedlings were considered emerged when the cotyledons were unfolded. After emergence was completed, the seedlings were thinned to single plants, 20 cm apart.

Subsequent growth of the seedling shoots was followed at weekly intervals by harvesting a 1-m section of row on seven successive dates. Leaf area measurements were made with a LI-COR LI-3000 leaf area meter. The plant material then was oven-dried to a constant weight at 80°C. In addition, frequent non-destructive measurements of canopy development were made for the KNO_3-treated and control plants ('6203' only) of the April planting. For each treatment, 30 random plants (five plants from each of six replicate plots) were measured throughout the season. Percent ground cover through day 50 was determined from photographs taken above the plants. Later in the season, the intercepted radiation was estimated by use of a line quantum sensor and a quantum meter.

Destructive harvests of 2-m sections of each plot occurred 128 and 137 days after planting for the March experiment and 112, 118, and 125 days after planting for the April experiment to assess possible differences in maturity between treatments. The harvested fruit were separated into red, green, and overripe classes and weighed. Soluble solids content and pH were determined from samples from the ripe fruit of the final harvest.

Statistical analysis. Final germination percentages at 10°, 20°, and 30°C were analyzed by analysis of variance (ANOVA) after arcsin of the square root transformation. Mean time to germination (T_{50}) was used to characterize the germination responses of each seed lot as affected by priming and temperature. The distribution of seed germination events over time was not normally distributed, but positively skewed. Consequently, the time factor was log- (base 10) transformed, which resulted in normally distributed germination responses over time (27). T_{50} then was calculated for each replicate using the transformed values. Variances for the different priming treatments were homogenous after this transformation (Bartlett's test), allowing ANOVA for significance of treatment effects within each cultivar and temperature.

Final emergence percentages were analyzed by ANOVA after arcsin of the square root transformation. Each planting date and cultivar was analyzed separately. Emergence percentages were calculated over the total number of seeds planted.

Field emergence time courses were analyzed by survival analysis (18), which describes the distribution of responses over time. The dispersion of emergence events over time intervals was characterized by three parameters: a) cumulative emergence curve or proportion of seeds emerged after each interval out of the total number of seeds planted; b) the probability density function, which estimates the probability for a seed to emerge in a given time interval and is equivalent to the slope of the cumulative emergence curve (26); and c) time to 50% emergence (T_{50}), determined by linear interpolation. The kinetic properties (probability density and T_{50}) of each treatment were estimated on the basis of the population of emerged (viable) seeds. All seeds that failed to emerge by the end of the emergence period were assumed to be dead. The mean U scores computed using a Wilcoxon test were used to rank treatment performance; more negative mean U scores indicate faster emergence (26).

Growth. The method of orthogonal contrasts was used to characterize the patterns of response of the logarithms of leaf area, shoot dry weight, or percent ground cover over successive dates. For each plot, the pattern of response was described by three statistically independent quantities: the overall mean, the slope of the linear regression (relative growth rate), and a quadratic contrast that measured the deviation from linearity. Treatment effects for each parameter then were tested by ANOVA.

Differences in earliness and total yield due to treatment and cultivar were tested for significance by ANOVA.

Results

Laboratory germination. Priming treatments did not influence significantly the final germination percentage of either cultivar in laboratory tests (data not shown). Final germination percentage was slightly higher for 'UC204' (98%) than for '6203' (95%), although not significantly so.

When germinated at 20° or 30°C, priming reduced the T_{50} for germination to 33% (KNO_3) and 50% (PEG) of control values for 'UC204' and to 44% (KNO_3) and 60% (PEG) of control values for '6203' (Table 1). The KNO_3 treatment consistently resulted in the most rapid germination. At 10°, the PEG treatment was of little benefit for either variety, while the KNO_3 treatment still reduced the T_{50} to 80% ('UC204') or 60% ('6203') of the control value (Table 1).

Emergence. Average daily soil temperatures at seed depth during the emergence period were between 12° and 17°C for the March planting, and between 12° and 22° for the April planting. In March, the soil temperatures were fairly consistent throughout the emergence period, while, in April, a warm period immediately after planting was followed by a prolonged period of cold, wet weather.

Seeds planted in flats of sterilized soil in a lathhouse (to experience ambient temperatures similar to those in the field, but without disease or soil structure stresses) emerged more rapidly when primed than when untreated (Table 2). As in the laboratory germination tests, the KNO_3-primed seeds emerged most rapidly, but the relative differences between treatments were reduced.

Table 1. Mean time to germination for primed (KNO_3, PEG) and untreated (control) 'UC204' and '6203' tomato seeds at 10°, 20°, and 30°C.

Cultivar	Treatment	Mean time to germination (hr)[z] Germination temperature (°C) 10	20	30
UC204	KNO_3	436 b[y]	26 b	17 c
	PEG	735 a	34 b	30 b
	Control	530 a	69 a	59 a
6203	KNO_3	396 b	33 b	18 b
	PEG	619 a	44 b	31 a
	Control	655 a	75 a	47 a

[z] Data are expressed as the antilog of the mean log hours to germination.
[y] Values within each temperature and cultivar separated by protected LSD test of log T_{50} values, $P = 5\%$.

Table 2. Mean emergence times (T_{50}) for primed (KNO_3, PEG) and untreated (control) 'UC204' and '6203' tomato seeds planted in a lathhouse in Mar. and Apr. 1984.

Cultivar	Treatment	Time to 50% of the final emergence (days) March	April
UC204	KNO_3	13.5 a[z]	10.8 a
	PEG	14.3 ab	11.9 b
	Control	15.1 b	13.0 c
6203	KNO_3	12.0 a	10.4 a
	PEG	12.8 b	11.3 b
	Control	14.2 c	14.1 c

[z] Values within each cultivar and planting date separated by protected LSD test, $P = 5\%$.

Differences in final emergence percentage in the field due to the priming treatments were seen only in the April planting, where priming with either KNO_3 or PEG increased percent emergence for the '6203' cultivar but not for 'UC204' (Table 3). The time required for emergence was reduced by priming with either KNO_3 or PEG at both planting dates (Table 3). As in the laboratory and lathhouse tests, the KNO_3 treatment consistently resulted in the shortest time to emergence. The kinetic parameters of emergence within a planting date did not differ significantly between cultivars; therefore, detailed results will be discussed only for '6203' for each planting date.

In the March experiment, emergence began on day 8 for the KNO_3-primed seeds, but was delayed until day 12 for the control seeds (Fig. 1A). Emergence rate (characterized by the probability density function) showed two peaks, with maxima for primed seeds occurring on days 11 and 14, and for control seeds on days 12 and 15 (Fig. 1B). This pattern was associated with cool weather around day 12, which slowed emergence. Seedlings from primed seeds emerged earlier and more uniformly than untreated seedlings in the April planting also (Fig. 2). By the 7th day after planting, none of the seedlings from untreated seeds had emerged, while seedlings from KNO_3- and PEG-treated seeds had reached 54% and 44% emergence, respectively (Fig. 2A). Emergence rate of primed seeds peaked on day 6, while control seeds had a lower maximum emergence rate, which was delayed until day 10 (Fig. 2B). The rapid germination of the primed seeds resulted in emergence during warm weather immediately following planting, while control seeds had not emerged and subsequently were delayed further by cold

Table 3. Field emergence responses for primed (KNO_3, PEG) and untreated (control) 'UC204' and '6203' tomato seeds planted in Mar. and Apr. 1984[z].

Planting date	Cultivar	Treatment	Final emergence (%)	T_{50} (days)	Mean score (U)
March	UC204	KNO_3	53.8 a[y]	14.2[x]	−158 a[w]
		PEG	57.5 a	14.1	−185 a
		Control	55.4 a	15.2	428 b
	6230	KNO_3	52.7 a	12.3	−516 a
		PEG	52.5 a	14.5	−107 b
		Control	50.3 a	15.8	462 c
April	UC204	KNO_3	85.6 a	6.8	−1866 a
		PEG	87.1 a	7.3	−1086 b
		Control	81.9 a	10.4	3121 c
	6203	KNO_3	69.3 a	6.7	−1449 a
		PEG	70.9 a	6.9	−730 b
		Control	42.0 b	10.8	3036 c

[z] Values are based on emergence counts in 5-m plots and are the means for five (March) and six (April) replications.
[y] Values within each planting date and cultivar separated by protected LSD test of arcsin-transformed values, $P = 5\%$.
[x] Significance of mean differences shown by U score in next column.
[w] More negative U score values indicate faster emergence. Significant differences by Wilcoxon test, $P < 0.05$.

weather. Nonparametric comparisons (mean U scores) indicated that the emergence distribution for each seed lot differed significantly from that of the other two (Table 3). With the exception of 'UC204' in the March trial, the KNO_3-treated seeds had significantly shorter emergence times than the PEG-treated seeds and controls, while PEG-treated seeds had intermediate emergence rates.

Growth. Plant growth, characterized by leaf area (LA) and dry weight (DW), followed essentially the same pattern of response for both cultivars and planting dates. Although cultivar means for DW and LA were significantly different for both planting dates, there was no interactive effect between cultivars and treatments for either parameter (data not shown). In the March experiment, the average DW of '6203' (early season cultivar) over the period ranging from day 39 to day 64 was 34% above the corresponding DW of 'UC204' (mid- to late cultivar), and in the April trial, 50% greater than 'UC204' over the period ranging from day 30 to day 44. Averaged over both planting dates, cultivar '6203' had 43% more leaf area than 'UC204' during the period considered.

Growth of the plants from primed seeds exceeded that of the corresponding controls throughout the period prior to flowering (Fig. 3). The rate of growth was more rapid in April than in March due to higher temperatures, but the response to the seed treatments was similar in the two plantings. After natural log-transformation, the DW and LA data for each plot were fitted to a linear model. For all treatment combinations, the slopes accounted for 95% to 99% of the total variability, indicating that growth was log-linear. However, there were no significant differences among the slopes, indicating that the relative growth rates were unaffected by the seed treatments. The significant differences that were detected in DW and LA due to seed treatments were entirely due to differences in emergence date.

Comparable results were obtained for canopy development: plants from primed seeds had larger canopies than the controls from day 22 to day 69 (Fig. 4), with the most-pronounced dif-

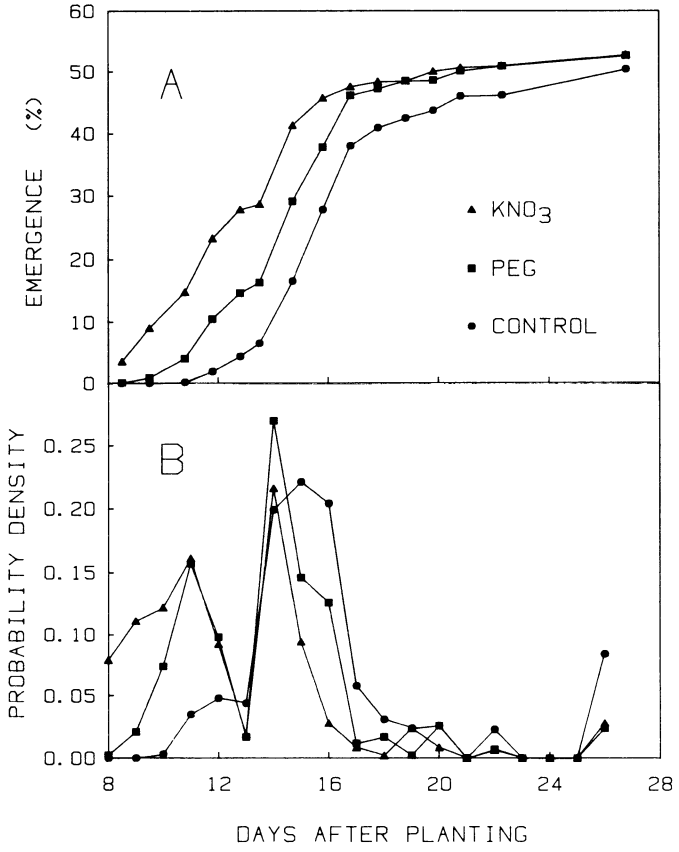

Fig. 1. Distribution of '6203' tomato emergence responses in a field planting in Mar. 1984. The priming treatments were in 3% (w/v) KNO_3 and −1.25 MPa PEG 8000. (**A**) Cumulative emergence time courses of primed and untreated tomato seedlings based on total number of seeds planted. (**B**) Emergence rates expressed as probability density functions derived from the curves of **A** and based on the number of emerged seedlings. The emergence rate of each treatment differed significantly from that of the other two (see Table 3).

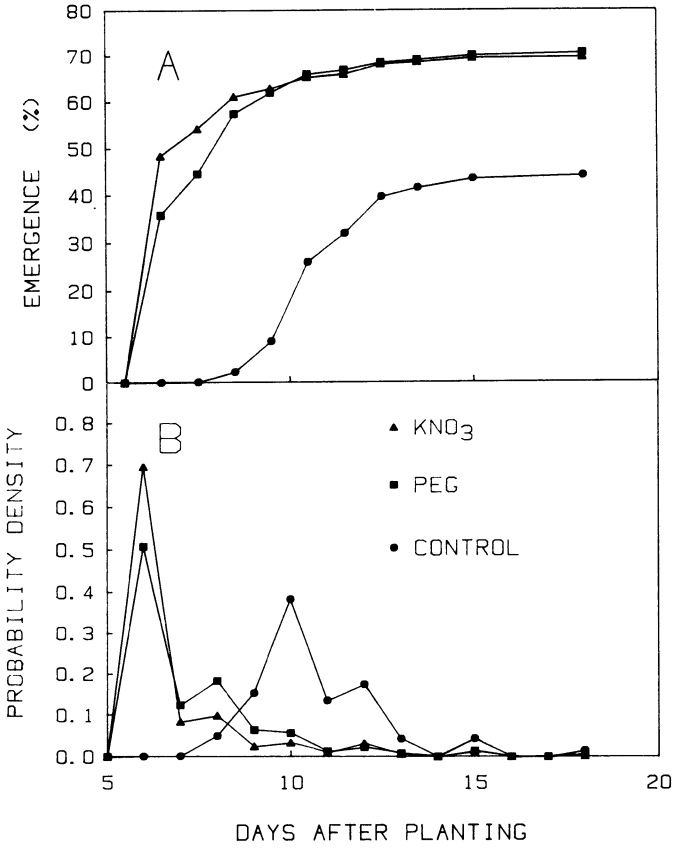

Fig. 2. Distribution of '6203' tomato emergence responses in a field planting in Apr. 1984. (**A**) Cumulative emergence. (**B**) Probability density. For details see Fig. 1. The emergence rates of each treatment differed significantly from that of the other two (see Table 3).

ferences occurring early in plant development. However, the relative rates of canopy expansion (slopes of the regression lines) did not differ (Fig. 4 inset).

Yield. Although the DW and percent ground cover of the primed seedlings was greater than for the controls during the early growth phase, no significant differences in earliness of maturity, fruit yield, or total aboveground plant DW were observed due to seed treatments (data not shown). Fruit soluble solids content and pH were not affected by the seed treatments.

Discussion

The results presented here confirm that, under laboratory conditions, tomato seeds primed in KNO_3 or PEG solutions can be dried back after pretreatment and still exhibit significantly reduced germination times relative to unprimed seeds. The promotive effect of seed priming was evident even at germination temperatures of 20° and 30°C, which are not considered stressful for tomato seeds. At the suboptimal temperature of 10°, only the KNO_3-primed seeds still exhibited enhancement due to priming. Although the primary effect of KNO_3 or PEG is to regulate the osmotic potential of the solution and prevent germination during the treatment, the KNO_3-primed seeds consistently exhibited the most rapid germination (Table 1). These results are in agreement with those of Bussell and Gray (9), who found that solutions of KNO_3 + K_3PO_4 were more effective than PEG solutions in reducing the time to germination of tomato seeds. On the other hand, Rumpel and Szudyga (23) observed increased seedling emergence from primed tomato seeds, but found no difference between PEG and KNO_3 + K_3PO_4 as osmotica. Penetration of ions into the seeds was suggested as causing deleterious effects of KH_2PO_4 treatment on germination of celery, leek, onion, and carrot seeds (6). Tomato seeds may be more tolerant of ion accumulation than are other seeds, as embryo K content is increased by 25% in tomato seeds primed in KNO_3 (K.J.B. and G.R. Cramer, unpublished data).

Seed priming significantly decreased the mean time to emergence in the field (Table 3; Figs. 1 and 2), in agreement with the results of Haigh et al. (13). As in the laboratory and lathhouse tests (Tables 1 and 2), seeds primed with KNO_3 as the osmoticum consistently exceeded the performance of PEG-treated seeds (Figs. 1 and 2). In spite of the early emergence of primed seeds, increased final emergence percentage was observed only in April for '6203', indicating that the risks associated with seedling establishment were not reduced in general as a result of shorter periods of exposure to adverse factors. Earlier seedling emergence from primed seeds compared to control seeds has been associated with improved stands in some studies (23), but not in others (13).

Seedlings from primed seeds achieved earlier canopy expansion than did control seedlings, resulting in greater leaf area and greater mean plant weights throughout the exponential growth period (Figs. 3 and 4). These results agree with those of Wolfe and Sims (30), who found that the advantage in emergence date in PEG-treated tomato seeds was maintained through early leaf

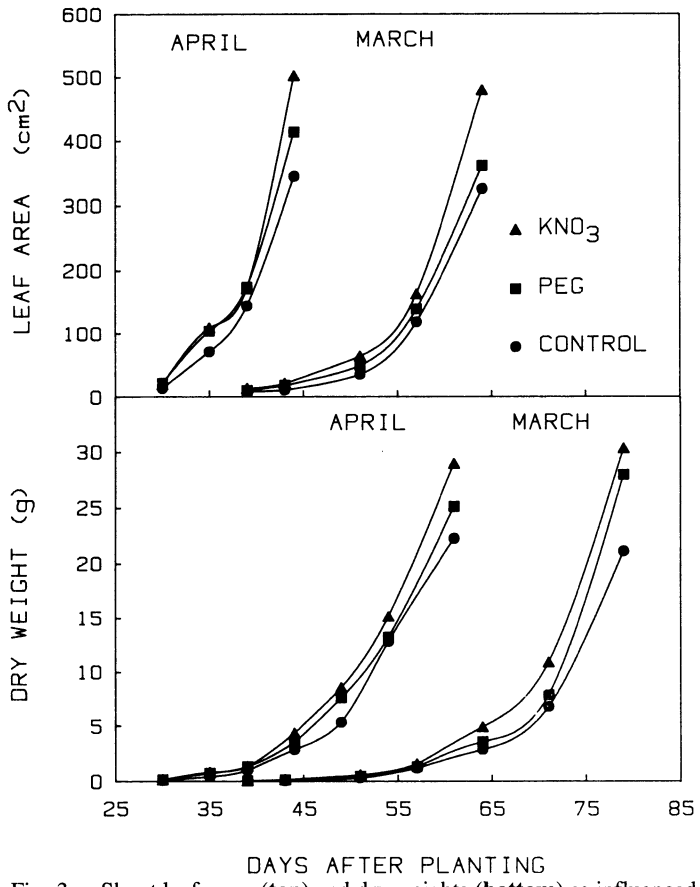

Fig. 3. Shoot leaf areas (**top**) and dry weights (**bottom**) as influenced by priming of '6203' tomato seeds in March and April plantings.

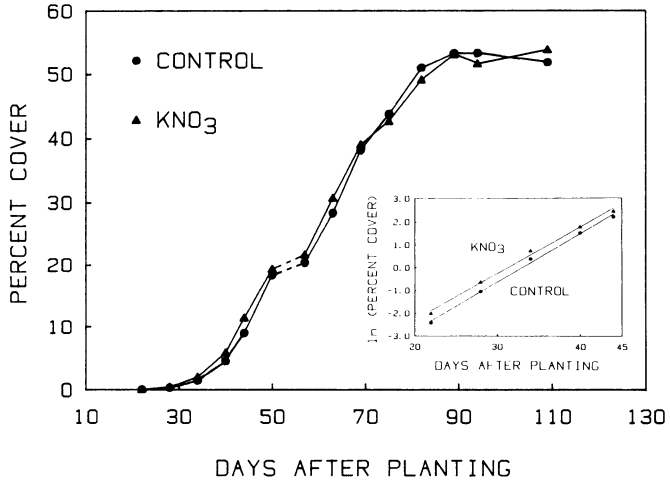

Fig. 4. Canopy expansion of '6203' tomato seedlings as influenced by seed priming treatments. Percent ground cover was determined on KNO_3-primed and control plants. Through day 50, measurements were taken from photographs. From day 57 through day 109, a quantum sensor was used to estimate canopy cover from light interception measurements. (**Inset**) ln percent cover through day 44. The regression lines for the two treatments have significantly different means, but identical slopes.

development (26 days after planting). It also concurs with results obtained for several other vegetable crops (5), where increased plant weights from primed seed resulted from early seedling emergence. However, priming treatments had no significant effect on the relative growth rate. Extension of the linear growth phase allowed the control plants to "catch up," resulting in no difference in final light interception due to priming (Fig. 4). There was also no increase in total dry matter production, harvestable yield, or fruit soluble solids content due to the treatments. A direct relationship between leaf area duration and total biomass production has been documented for many crops (1, 22, 25). Integration under the curves of Fig. 4 indicates that total light interception over the season differed by only 2% between the treatments. Thus, the advantage in leaf area duration due to 4 days earlier emergence was small relative to the total seasonal light interception. In addition, if the photosynthetic capacity of processing tomatoes is ample, as suggested by Hewitt and Marrush (16), an increase in leaf area duration might not increase yield of fruits, although total dry matter production might still increase.

Although flowering occurred earlier in primed plots than in control plots (data not shown), this was not reflected in earlier fruit maturity. The similarity of maturity dates was likely due to hot weather, which advanced ripening by as much as 2 weeks and compressed the spread of harvests among different planting dates. In addition, extremely high temperatures at flowering greatly reduced initial fruit set, where the advantage due to priming would have been most evident. In crops with relatively short growth periods from which the vegetative organs are harvested, earlier emergence of primed seeds relative to untreated seeds has resulted in earlier maturity or increased yields—i.e., carrots (2, 5, 24, 28), onions (5, 18), and lettuce (11). In tomatoes, 7- to 8-day reductions in T_{50} due to fluid drilling of pregerminated (29) or primed (30) seeds resulted in 10% to 12% increases in the percentage of red fruit at harvest but no significant increases in total yield. Considerable reductions in emergence time are apparently required in tomato to realize earliness at maturity due to the long period of growth and the requirement for pollination and fruit set (8, 12).

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J. Amer. Soc. Hort. Sci. 112(3):432–436. 1987.

Salinity Effects on Asparagus Yield and Vegetative Growth

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Additional index words. *Asparagus officinalis*, salt tolerance, seedling growth, germination, osmotic potential, total soluble solids

Abstract. **The effect of salinity on germination, first-year growth, and spear and fern yield of asparagus (*Asparagus officinalis* L.) was determined in germination dishes, crocks, and field plots, respectively. Saline treatments were imposed by irrigating with water that contained equal weights of NaCl and $CaCl_2$. Spear yield was reduced 2.0% for each unit increase in salinity above 4.1 $dS \cdot m^{-1}$. Yield reduction was attributed primarily to a reduction in individual spear weight. Mature asparagus plants would be considered the most salt-tolerant crop commercially available. Asparagus possessed nearly the same salt tolerance for germination and spear production with soil salinities <7.2 $dS \cdot m^{-1}$. Above 7.2 $dS \cdot m^{-1}$, germination was less salt-tolerant. First-year growth was significantly more salt-sensitive than growth in subsequent years.**

Asparagus (*Asparagus officinalis* L.) has been found growing wild in so many places that its place of origin is doubtful. However, there seems to be a consensus that it originally was native to the eastern Mediterranean seacoast of Europe, North Africa, and Asia (1, 8). Recorded history indicates that it has been cultivated in this region for more than 2000 years. The Roman historian, Marcus Porcus Cata, wrote a full-length discourse on asparagus cultivation in his *De Re Rustica* in about 161 BC (16). Not only was it prized as a food but was valued for its medicinal properties as well. Supposedly it could cure everything from bee stings to heart trouble and toothaches (8).

Asparagus is believed to have been introduced into the United States by the immigration of Huguenots from France in the 1600 and 1700s (16). However, it was not grown commercially until about 1850 to 1860. Today, it has become one of the most important perennial vegetable crops grown in the United States (8).

In the early days of its cultivation in the United States, the application of salt on asparagus fields was nearly universal. Apparently, gardeners believed that since asparagus was native

Received for publication 12 May 1986. I thank Frank H. Takatori, Univ. of California, Riverside, for his helpful advice in the initiation of this study. Appreciation is also extended to Michael C. Shannon for osmotic potential and total soluble solids measurements and Donald A. Layfield for elemental analyses of the plant tissues. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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