Effect of Irrigation, Soil Matric Potential, and Seed Priming on Sugar Beet Seed Germination and Damping-Off Caused by *Aphanomyces cochlioides*

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Accepted for publication 12 November 1992.

ABSTRACT

Rush, C. M., and Vaughn, K. M. 1993. Effect of irrigation, soil matric potential, and seed priming on sugar beet seed germination and damping-off caused by *Aphanomyces cochlioides*. Phytopathology 83:202-206.

Laboratory studies were conducted to evaluate how seed priming and soil matric potential affect sugar beet seed germination. Seed treatments included solid matrix priming (SMP), SMP + hydroxyethyl cellulose (HEC) hydrated to form a viscous fluid, and an untreated control. Seed were planted in soils with matric potentials ranging from −100 to −700 J kg^{-1}. Evaluations of seed germination and radicle length were made at 2, 3, 4, 5, and 7 days after planting. Soil matric potential had only minimal effect on seed germination and radicle elongation as determined by regression analysis for individual treatments and times after planting. Conversely, seed treatments greatly influenced germination. There was no significant seed treatment × matric potential interaction. At 2 days after planting, seed germination, averaged across all matric potential treatments, was 72, 34, and 1% for the SMP + HEC, SMP, and control treatments, respectively. Mean radicle lengths for the same treatments were 3.3, 1.2, and 0.1 mm. By day 7, differences in germination among seed treatments were minimal, but significant differences in radicle length were found. These same seed treatments were used in a greenhouse study to determine how irrigation affected Aphanomyces seedling disease. Seed of each treatment were planted in soil, contained in 10 wooden boxes (1- × 2-m), that was artificially infested with oospores of *Aphanomyces cochlioides*. All boxes were flood-irrigated approximately 10 days before planting; after planting, five of the boxes were irrigated again. Soil water content, seedling emergence, and seedling damping-off were monitored for 3 wk. Seedlings from SMP and SMP + HEC seed treatments emerged significantly earlier than untreated seed, but no seed treatment affected seedling disease. However, irrigation treatment greatly affected disease incidence. In the five boxes that received postplant irrigation, mean seedling disease, averaged across all seed treatments, was 41%, but in the five boxes that received only a preplant irrigation, mean disease incidence was significantly lower, at 7%. Analysis of soil dry-down curves from the two irrigation treatments revealed that soil that received only a preplant irrigation was too dry 5 days after planting for zoospore movement. These results indicate Aphanomyces seedling disease can be significantly reduced by planting into soil wet enough for seed germination but too dry for zoospore movement.

In the Texas Panhandle, *Aphanomyces cochlioides* Drechs. is the primary cause of sugar beet (*Beta vulgaris* L.) seedling disease. Currently, no fungicides approved in the United States are effective against this pathogen, and no cultivars have adequate resistance. The only recommendations given to Texas growers for management of this disease are to plant early when soils are cool and to irrigate only once after planting for stand establishment. *A. cochlioides* is a warm-temperature pathogen, and early planting can be quite effective in suppressing stand losses to blackroot (23). However, cool, wet soils can favor seedling disease caused by other pathogens, such as *Pythium* spp. Likewise, a single postplant irrigation for stand establishment can result in soil crusting, which may affect emergence more than may seedling disease (16). Therefore, multiple irrigations for establishing an adequate stand are not uncommon, but the excessive soil water is conducive for dispersal and infection by zoospores.

Over the last few years, several researchers have evaluated effects of seed priming to determine effects on sugar beet stand establishment and seedling disease. Seed priming is a treatment in which the germination process is initiated and stopped before radicle emergence. This is achieved by regulation of the water potential (ψ) of the imbibition medium. Water potential of the imbibition medium can be controlled by regulation of osmotic potential (ψ_s), matric potential (ψ_m), or a combination of the two (1,11,22,24). Priming increases earliness and uniformity of sugar beet seedling emergence (10,19,22) and suppresses losses to seedling damping-off caused by *Pythium ultimum* Trow (15, 21,22,24,25). Protection against *P. ultimum* has been attributed to escape, reduction in seed exudates, and an increase in indigenous bacteria on primed seed (17,18,22). Although seed priming can reduce loss to seedling infection by *P. ultimum*, seedling disease caused by *A. cochlioides* is not affected (25). *A. cochlioides* typically infects the hypocotyl of sugar beet seedlings after emergence and is dependent on near-saturation soil conditions for infection (4,5,20,23). Therefore, factors that influence seedling infection by *P. ultimum*, such as seed exudates and germination rate, are unlikely to affect *Aphanomyces*. However, because *A. cochlioides* is dependent on high levels of soil moisture for seedling infection, disease control through irrigation management is conceivable. If seed could be planted into a soil moist enough for seed germination but too dry for movement of zoospores, disease might be avoided. Since primed seeds germinate faster than untreated seeds in wet soils, primed seeds might also germinate better in relatively dry soils than in wet (2,3). On this premise, a study was initiated to determine if the priming of sugar beet seed improved germination and growth in soils of various matric potentials, and if Aphanomyces seedling disease could be reduced by irrigation management.

MATERIALS AND METHODS

Laboratory study. Subsamples, approximately 500 g each, of a heat-pasteurized Pullman clay loam soil were adjusted to −100, 300, 500, or 700 J kg^{-1} with positive air pressure and porous ceramic plates. After equilibrating in pressure chambers, the four soils were placed in plastic bags until use, usually within 24 h.

Three seed treatments were used in this study: solid matrix priming (SMP) (11), SMP + hydroxyethyl cellulose (HEC) hydrated to form a viscous gel, and an untreated control. Solid matrix priming was performed as previously described (24). Sugar beet seed were mixed with a dry hydrous silicate clay and water at approximately 1:1:1 by weight and incubated for 5 days at 15 C. For SMP + HEC treatment, SMP seed were hydrated with water at 15 C for 2 h immediately before use. HEC, 2.2 g, was mixed with 100 ml of warm water, 32 C, and the suspension was stirred until it became viscous. Approximately 30 ml of the hydrated HEC was mixed with 15 g of hydrated SMP seed before

planting.

A total of 10 seeds from each treatment were placed in a Y plate, (i.e., a compartmented petri plate) and covered with soil of a given matric potential. Plates were sealed to maintain moisture content. A total of 25 plates were prepared for each soil treatment, and all plates were incubated in the dark at 15 C. At 2, 3, 4, 5, and 7 days after initiating the study, five plates from each soil treatment were collected to evaluate soil and seed treatment effects on germination and radicle length. Results were expressed as percent seed germination and mean radicle length over time.

Moisture release curves. These curves were developed for greenhouse and field soils. Soils on porous ceramic plates were saturated with distilled water, and then positive air pressure equal to a given potential was applied. After reaching equilibrium, gravimetric water content was determined, and a graph of gravimetric soil water content versus soil matric potential in J kg^{-1} was developed. These curves were then used to determine soil matric potentials reported in this study.

Greenhouse study. The greenhouse study was conducted to determine if Aphanomyces seedling disease could be suppressed by limiting irrigations at planting time. Ten wooden boxes (2 × 1 × 0.3 m) filled with unsterile Pullman clay loam were flood-irrigated approximately 10 days before planting. The same seed treatments used in the laboratory study (i.e., SMP, SMP + HEC, and untreated control) were included in the greenhouse study. Three shallow trenches, approximately 1–2 cm deep, were made across the width of each box, and 30 g of *Aphanomyces* oospore inoculum (25) was added to each trench. A total of 50 seeds from each treatment were then placed in the trenches, covered with soil, and lightly tamped. Seed from the SMP + HEC treatment were mixed with 50 ml of hydrated HEC, placed in a 60-cm^3 syringe, and injected into the trench. Of the 10 boxes, five then received a second irrigation immediately after planting. No additional water was added to any of the boxes for the duration of the experiment. Each box was considered a replication. Soil samples to determine gravimetric soil water content were taken the day of planting from the five boxes that received only preplant irrigation. Samples were taken daily for the next 10 days from all 10 boxes. A previously developed moisture release curve was used to convert gravimetric values to J kg^{-1}, and all soil moisture measurements were recorded as soil matric potential.

Seedling emergence and postemergent damping-off were recorded daily for the first 10 days of the study, and then damping-off was recorded every other day for an additional 2 wk. Any seedling that exhibited typical blackroot symptoms (i.e., water-soaked, discolored hypocotyl [20]), was counted as damped-off and was removed from the box.

Data analysis. Laboratory and greenhouse studies were repeated once. Repeated-measures ANOVA was used to analyze results from laboratory and greenhouse studies. In both studies, there was a significant ($P = 0.05$) treatment × time interaction, so treatment means were analyzed for each time separately. In the laboratory study, soil water potential was the main plot, and seed treatment was the subplot. Some of the laboratory data were subjected to regression analysis to determine the relative importance of soil water potential and time on seed germination and radicle growth. In the greenhouse study, irrigation was the main plot, and seed treatment the subplot. Homogeneity of variances between separate tests was determined by Bartlett's test for homogeneity. When variances were homogeneous, and no seed treatment by water potential or irrigation interaction existed, data were usually merged and presented as seed treatment effect. All analyses were conducted with Statistical Analysis System for personal computers (SAS Institute, 1988).

TABLE 1. Coefficient of determination values (R^2)[x] for linear regression of soil matric potential with seed germination (G) or radicle elongation (R) for specific sampling days and seed treatments[y]

Days after planting	Seed treatments[z]					
	Control		SMP		SMP + HEC	
	G	R	G	R	G	R
2	0.03	0.03	0.08	0.07	0.05	0.01
3	0.09	< 0.01	0.06	0.01	0.02	0.05
4	< 0.01	< 0.01	0.06	0.06	0.02	0.02
5	0.11*	0.14**	< 0.01	0.13*	< 0.01	0.21**
7	< 0.01	0.26**	0.01	0.05	0.04	0.10*

[x] All R^2 values are for linear equations. Data were subjected to nonlinear regression, but typically, there was little or no improvement of the R^2 value. An * indicates significance at $P = 0.05$, and ** indicates significance at $P = 0.01$.

[y] ANOVA indicated no significant difference between repeated tests, and variances were homogeneous, so data were merged for all analyses.

[z] Treatments included soil matrix priming (SMP), SMP plus hydrated hydroxyethyl cellulose (SMP + HEC), and an untreated control.

RESULTS

Laboratory Study. Variances between repeated tests were homogeneous, and ANOVA indicated no significant differences between repeated tests or test × treatment interactions, so results were merged for further analysis. ANOVA and regression analysis both indicated that soil water potential had only minimal effect on seed germination or radicle elongation. There was a significant seed treatment × day interaction, so R^2 values of linear regression for soil matric potential effects on germination and radicle length at each separate sampling date and for each seed treatment were determined (Table 1). Given the results of regression analysis, radicle elongation was more sensitive than germination to soil water potential. However, significant R^2 values were only obtained at 5 and 7 days after planting, and these were very low.

Although soil water potential had minimal effect on seed germination and radicle elongation, seed treatments greatly affected these variables. The seed treatment × soil water potential interaction was not significant, so data were merged and results presented as seed treatment effects (Figs. 1 and 2). Seed germination was greatly enhanced by the SMP treatment and even more so by SMP + HEC. Within 48 h after planting, 72% of the SMP + HEC–treated seed had germinated, whereas only 1% of the untreated seed had germinated (Fig. 1). Even after 7 days, untreated seed had germinated significantly less than SMP + HEC–treated seed. SMP-treated seed germinated as well as the SMP + HEC–treated seed by day 4 and significantly better than untreated seed until day 7. Radicle elongation was also significantly affected by seed treatments (Fig. 2). At each sampling

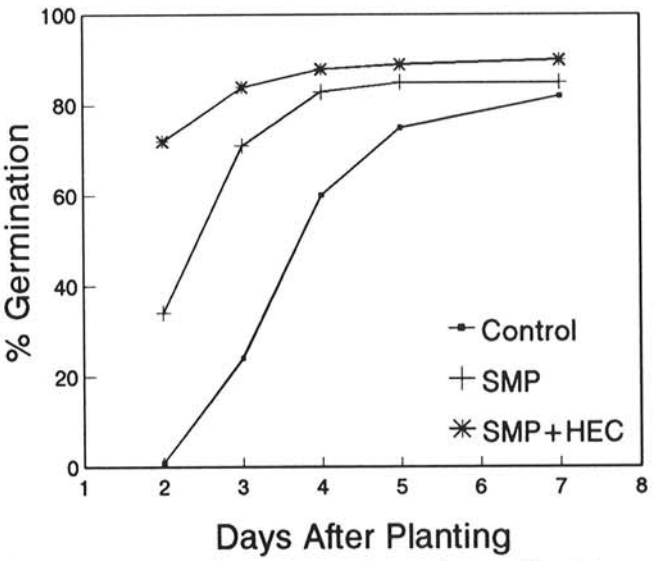

Fig. 1. Germination of sugar beet seed over time as affected by seed treatments. There was no seed treatment × water potential interaction, so data were merged and presented as seed treatment effect. Repeated-measures ANOVA indicated a significant time × treatment interaction, so data from each day after planting were analyzed separately. LSD values for days 2, 3, 4, 5, and 7 are 7.2, 7.4, 6.8, 5.4, and 6.4, respectively.

date, radicle lengths among the three seed treatments were all significantly different with SMP + HEC > SMP > control. By day 7, mean radicle length of SMP or SMP + HEC–treated seed was approximately two and three times that of the untreated control, respectively.

Greenhouse study. Results from repeated greenhouse tests were different, and significant test × treatment interactions existed, so results were not merged. However, within tests, no significant seed treatment × irrigation interaction existed, so these data were merged and presented either as seed treatment effect or irrigation effect.

Seed treatments had only minimal effects on stand establishment and no effect on disease incidence (Table 2). Only at day 3 in the first test did seed treatments affect emergence. However, irrigation treatments significantly affected emergence and disease (Table 3). In both tests, stands were significantly greater at every count with postplant irrigation than with preplant. Although differences between stands in postplant- and preplant-irrigated boxes were always statistically significant, differences at day 6 were minimal and, from a practical point of view, probably insignificant.

Irrigation had major effects on disease, especially in the first test (Table 3). In both tests, incidence of disease was significantly greater in boxes that received a postplant irrigation than in those that did not, but in the first test there was an 11-fold difference between treatments. The difference in disease development between seedlings given the different irrigation treatments can be explained, in part, by differences in soil matric potential (Fig. 3). Soils that received postplant irrigation never dried past −50 J kg^{-1}, but soil in boxes that received only a preplant irrigation dried to −200 J kg^{-1} by day 6. In the second test, soil dry-down curves for the two irrigation treatments were similar to those in the first test, but inexplicably the incidence of seedling disease was much less (Table 3). Still, the amount of seedling disease with postplant irrigation was three times greater than that with preplant irrigation only.

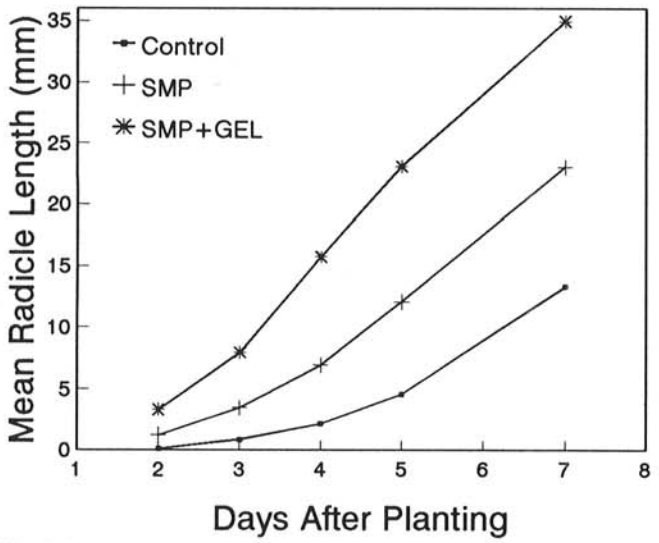

Fig. 2. Seed treatment effects on radicle elongation. There was no seed treatment × water potential interaction, so data were merged and presented as seed treatment effect. Repeated-measures ANOVA indicated a significant time × treatment interaction, so data from each day after planting were analyzed separately. LSD values for days 2, 3, 4, 5, and 7 are 0.41, 0.58, 1.3, 1.9, and 3.1, respectively.

TABLE 2. Seed treatment effects on stand establishment and seedling disease

Seed treatments[x]	Emergence (%) Day 3 Exp. 1	Emergence (%) Day 3 Exp. 2	Emergence (%) Day 6 Exp. 1	Emergence (%) Day 6 Exp. 2	Disease (%)[y] Exp. 1	Disease (%)[y] Exp. 2
SMP	77 a[z]	89 a	99 a	94 a	33 a	19 a
SMP + HEC	85 a	84 a	100 a	87 a	35 a	19 a
Control	23 b	89 a	99 a	95 a	26 a	19 a

[x] There was no significant seed treatment × irrigation interaction, so means represent seed treatment effect inclusive of irrigation treatments. SMP = soil matrix priming; HEC = hydrated hydroxyethyl cellulose.
[y] Based on number of plants emerged after day 6 that became infected.
[z] Means within a column followed by the same letter are not significantly different according to Duncan's multiple range test ($P = 0.05$).

DISCUSSION

The primary question at the outset of this research was whether Aphanomyces seedling disease could be avoided by planting seeds into soil too dry for zoospore movement but wet enough for seed germination. Our findings support the feasibility of the basic concept, but results concerning ψ_m effects on seed germination were in some ways dissimilar to previously published reports (3,6,14). In this study, neither rate of seed germination nor radicle elongation was observed to be affected by ψ_m. Conversely, Gummerson (14) found that rate of sugar beet germination was affected by ψ_s, ranging from 0 to −1,200 J kg^{-1}, at each of five temperatures. Similarly, Bradford (3) found that reductions in ψ_s of −200 J kg^{-1} delayed germination of lettuce. However, in agreement with the present study, both Gummerson and Bradford reported that although germination rate was suppressed by minimal changes in ψ_s, final germination percentages were not suppressed until ψ_s was <−1,000 J kg^{-1}.

The apparent discrepancies between the present study and previously published reports can be readily explained by differences in research objectives and methodology. In previous studies

TABLE 3. Irrigation treatment effects on stand establishment and seedling disease

Treatments[x]	Emergence (%) Day 3 Exp. 1	Emergence (%) Day 3 Exp. 2	Emergence (%) Day 6 Exp. 1	Emergence (%) Day 6 Exp. 2	Postemergent damping-off (%)[y] Exp. 1	Postemergent damping-off (%)[y] Exp. 2
Postplant	59 a[z]	96 a	100 a	99 a	56 a	27 a
Preplant	41 b	76 b	96 b	87 b	5 b	9 b

[x] There was no significant seed treatment × irrigation interaction, so means represent irrigation effect inclusive of seed treatments.
[y] Based on number of plants emerged after day 6 that became infected.
[z] Means within a column followed by the same letter are not significantly different according to Duncan's multiple range test ($P = 0.05$).

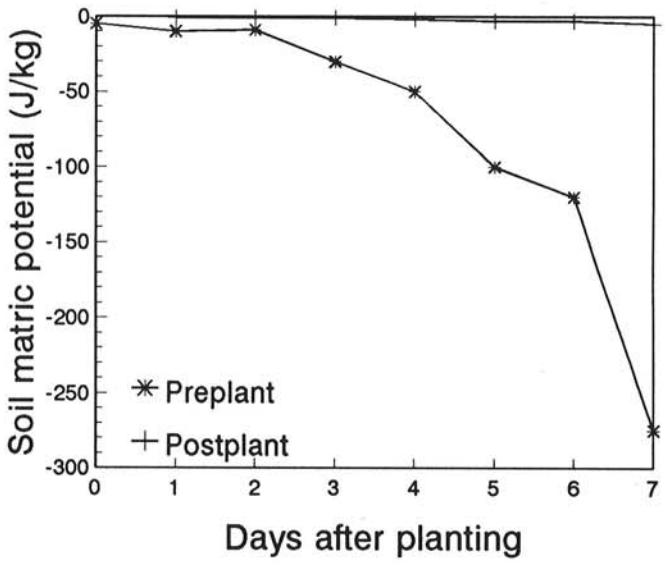

Fig. 3. Dry-down curves for soils in the greenhouse study that received only a preplant irrigation or a pre- and postplant irrigation. Points represent the mean of five replicates. Differences in matric potential between the two irrigation treatments were significant ($P = 0.05$) after day 2.

(3,14), Bradford and Gummerson were interested in defining and modeling the effect of ψ on germination and germination rate. Both regulated ψ osmotically, and seeds were checked every 2–3 h for germination during incubation at different ψ_s. In the present study, the primary concern was not with effect of ψ on rate of germination, but on final percent germination. Matric potential was used to regulate ψ, and the first evaluation of germination was made after 48 h and at 24-h intervals thereafter. If seed had been checked earlier and more frequently, differences in rate of germination as affected by ψ_m may have been observed. However, as suggested by Gummerson, results of germination studies employing osmotic regulation of ψ may not necessarily pertain to situations in which matric potential is the main component of ψ (14).

Although rate of germination was not the primary focus of the present study, it is of primary importance to the concept of planting and establishing a stand in relatively dry soils. A typical soil dry-down curve for a Pullman clay loam soil is illustrated in Figure 4. The top 2.5 cm of the soil surface stays relatively wet for only a few days after an irrigation before it rapidly dries. However, soil just below the surface crust stays wet for a prolonged period. Since sugar beet seeds are typically planted only 2–3 cm deep, rapid germination and radicle extension into deeper, wetter soil are critical if a stand is to be established without postplant irrigation. In this study, the SMP and SMP + HEC seed treatments resulted in significantly earlier germination and radicle elongation than the untreated control at every ψ_m. Similar observations and models predicting priming affects on seed germination in relatively dry soils have been reported by others (2,6,10).

It was encouraging that seeds were capable of germinating and growing at relatively low ψ_m, but with regard to zoospore infection, evaluations of seed germination at $\psi_m < -100$ J kg^{-1} were primarily academic. Effects of both ψ_s and ψ_m on zoospore release and movement are well documented (7,12,13,26,27,29). Zoospores require nearly saturated soil conditions for movement, because the large soil pores through which they move drain at relatively high ψ_m (8,9). Even relatively small pores (~40–60 μm) drain at ψ_m of -2.4 to -3.6 J kg^{-1} (28). Therefore, zoospores are probably unable to move through soil at $\psi_m < -100$ J kg^{-1}. This hypothesis is supported by numerous publications in which zoospore infection was reported to be negligible at $\psi_m < -20$ J kg^{-1} (7,8). In the present study, disease development on sugar beet seedlings was greatly suppressed in soils that received only a preplant irrigation. The ψ_m in these soils decreased to < -50 J kg^{-1} within approximately 4 days after planting. Zoospores, the infective unit of *A. cochlioides*, typically infect the hypocotyl of seedlings after emergence (20), so the period during which soils were wet enough for zoospore movement was brief. This period was considerably longer in soils to which postplant irrigation was applied. Consequently, the incidence of infection was also much greater in postplant- than in preplant-irrigated soil. Even though percent infection of seedlings was low in soils that received only a preplant irrigation, infection was still greater than expected, because of the relatively low ψ_m. Oospore inoculum was placed with the seed, so hypocotyls may have been in direct contact with germinating oospores, and subsequently, zoospores were not required to move to the infection court.

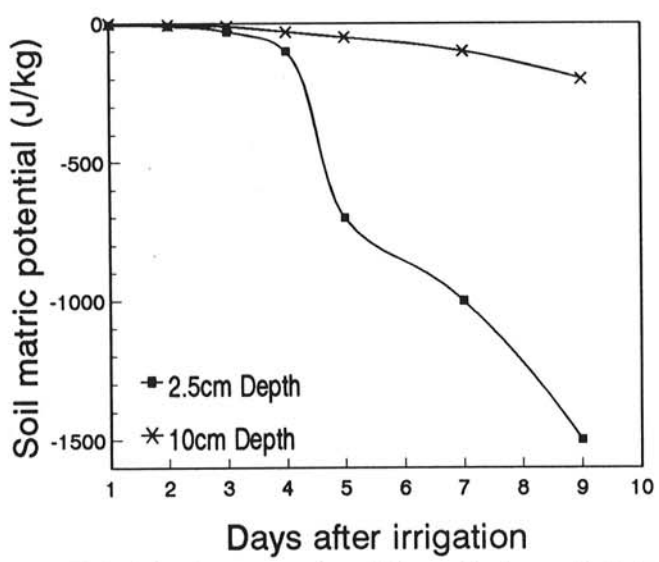

Fig. 4. Typical dry-down curves for a Pullman clay loam soil. Points represent the mean soil matric potential of five samples taken from a depth of 2.5–10 cm. Differences between sampling depths were significant ($P = 0.05$) after day 4.

In conclusion, the concept of avoiding seedling disease, caused by *A. cochlioides*, by planting into a soil too dry for movement of zoospores seems to be feasible. Results from the greenhouse study are encouraging, but field studies are required for final proof. The major obstacle to avoiding disease by irrigation management is achieving seed germination and radicle extension before the soil dries in the planting zone. The use of primed seed to speed germination in drying soil should help. If this system works, it will be an effective, inexpensive, and environmentally sound method of managing this disease.

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