Soil Water Potential Requirement for Germination of Winter Wheat

Stewart B. Wuest*
USDA-ARS
Columbia Plateau Conserv. Res. Center
Pendleton, OR 97801

Larry K. Lutcher
Dep. of Crop and Soil Science
Oregon State Univ.
Morrow County Ext.Office
Heppner, OR 97836

In semi-arid climates, seed is often sown into soil with inadequate water for rapid germination. Distinguishing between adequate and marginal water can be difficult. Planting decisions become increasingly complicated when one considers possible differences between cultivars. This study was designed to measure the soil water potential limits for rapid, adequate, and marginal germination of winter wheat (*Triticum aestivum* L.). Laboratory data showed that germination was rapid (3 to 4 d) in soil at water potentials above -1.1 MPa and slower (4 to 5 d) at water potentials that ranged from -1.1 to -1.6 MPa. Below -1.6 MPa, less than half of the experimental units achieved the cut-off criteria of 75% germination with 5-mm radical length within 25 d. Six cultivars varied in time to germination by an average of 0.34 d, and two randomly selected seed lots of each cultivar differed by an average of 0.20 d. We conclude that variation between seed lots may be as important as variation between cultivars when looking for seed with superior germination under marginal soil water contents.

In semi-arid ecosystems, the soil water content is often too dry for rapid germination of seed. Some agricultural systems depend on planting into marginal soil water as a way of outcompeting weeds or for establishing annual winter grasses in the fall. Winter wheat producers in low precipitation areas of the Pacific Northwest, United States, use a 13- to 14-mo period of fallow to control weeds and store water before planting. Maximum yields are produced from late August to mid-September plantings. If seed-zone water is marginal or inadequate for germination, then germination is delayed until the onset of fall rains in October or later. The yield penalty associated with delayed planting can be significant (Donaldson et al., 2001; Giri and Schillinger, 2003) and is influenced by weather and management techniques (Lutcher et al., 2010; Higginbotham et al., 2011).

Research has established that many species can germinate at soil water potentials well below those that maximize plant growth (Owen, 1952). At water potentials from zero to approximately -1.0 MPa, where the soil atmosphere begins to drop below 99% relative humidity (Papendick and Campbell, 1981), the germination rate is near maximum (Rogers and Dubetz, 1980; Blackshaw, 1991). Further decreases in water potential slow the speed of germination, and when the soil becomes too dry, germination halts or is so slow that pathogens infect the seed. Pawloski and Shaykewich (1972) showed that these effects were similar between soils, even when the soils differed in hydraulic conductivity by a factor of 10.

An important crop production question is whether it is possible to select cultivars that can germinate and grow at lower water potentials than the average cultivar.

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*Corresponding author (stewart.wuest@ars.usda.gov).

Helmerick and Pfeifer (1954) used field observations to select two wheat cultivars, which seemed to have the best and worst emergence under water stress conditions. Each cultivar was represented by two seed lots grown at the same two locations to test the effect of seed source. Their results showed significant differences in cultivar performance, especially at low water potentials, but no difference between seed lots. It is possible that the seed lot similarity in this one comparison of seed grown at two locations is not typical of seed lots in general. For example, Hrstkova et al. (2006) studied seed lots of barley (*Hordeum vulgare* L.) grown at six locations and found significant effects of both seed lot and cultivar on germination, especially under water stress.

If growing conditions during seed production affect germination performance, we would expect seed lots to differ depending on the location and year of production. Seed can also differ in germination performance due to seed size (Lafond and Baker, 1986; Aparicio et al., 2002; Willenborg et al., 2005) and storage conditions (Niedzielski et al., 2009).

Except for a few well researched soils, there are no well-defined criteria for determining if a soil contains a high enough water content to germinate wheat. The goal of the study described here was to produce guidelines for predicting the performance of a wheat planting operation given the seed-zone water content and the soil water potential characteristics. Conditions allowing rapid germination are also likely to allow emergence and root growth, assuming that the soil does not dry further after planting. Lindstrom et al. (1976) measured little change in water content at planting depth after deep seeding into tilled summer fallow, but there are observations to the contrary. The research reported here did not investigate soil water changes in the field after planting.

Etherington and Evans (1986) and later Wuest et al. (1999) used a simple technique for exploring the effect of soil water potential on germination. The method used a petri dish filled with moist soil, seed placed on top of the soil, and a lid sealed on top of the seed. The dish was slightly overfilled with soil so the seed would be held securely between the lid and soil and remain visible for periodic inspection. A thin layer of porous material like fiberglass filter paper on top of the soil aids in seeing radical development and does not interfere with water imbibition or germination timing since the major form of water movement to the seed is vapor (Wuest, 2007). The filled dishes can be handled without soil movement, and it is recommended to incubate with the lid side down so that the radical will grow toward the lid and be easier to see.

We hypothesized that the critical water potential for rapid and complete germination of winter wheat would be somewhat below -1.0 MPa. As a secondary goal, we hypothesized that cultivars, and seed lots of the same cultivar, might differ in their germination response at marginal water potentials. We did not attempt to identify what the causes of any lot-to-lot difference might be.

MATERIALS AND METHODS

This experiment used six cultivars, two seed lots, three soils, and two temperatures to evaluate germination rates at relevant water potentials. The six semi-dwarf, soft white winter wheat cultivars (Bruehl, Eltan, ORCF-102, Skiles, Stephens, and Tubbs 06) were developed for the Pacific Northwest region and account for 90% of planted acreage. Untreated seed of each cultivar was acquired from two randomly-selected and unassociated sources. Seed was dried at 35°C for 7 d to ensure an initially-uniform water content. Soils used in this experiment were a Shano silt loam (coarse-silty, mixed, superactive, mesic Xeric Haplocambid) containing 31% fine to very fine sand, 63% silt, and 6% clay; a Ritzville silt loam (coarse-silty, mixed, superactive, mesic Calcidic Haploxeroll) containing 32% fine to very fine sand, 60% silt, and 8% clay; and a Walla Walla silt loam (coarse-silty, mixed, superactive, mesic Typic Haploxeroll) containing 22% fine to very fine sand, 65% silt, and 13% clay. The temperatures of 20 and 15°C are typical of early (August) and normal (September) seeding dates at a 10-cm soil depth (Lindstrom et al., 1976, Lafond and Fowler, 1989).

Experimental Design

Soil water potentials were estimated from water release curves generated using both Tru Psi and WP4 psychrometers (Decagon Devices, Pullman, WA). Then four subsamples of each soil were adjusted to gravimetric water contents that coincided with water potentials ranging from -0.6 to -2.0 MPa. This produced a total of 12 soil-by-water content combinations. We did not attempt to match water potentials among soil types. Our goal was to have a few samples with water contents suitable for rapid germination, some that were too dry for germination, and several that were somewhere between the two extremes.

Final determination of each of the 12 soil water potentials was based on the average of four soil samples taken during the dish assembly process. Since we had a limited amount of soil water in each dish and were adding dry seed, we knew that the soil water potential would drop a substantial amount in the first 24 h as the seed equilibrated. To get a more accurate estimate of the resulting soil water potential inside the dish, we subtracted an approximate amount of water absorbed by the seed in the first 24 h, 17 mg per seed, from the measured water content of each dish. This was an approximate adjustment derived from earlier research (Wuest, 2002) and based on an average of 70 g dry soil per dish. The adjusted gravimetric water content was used to estimate water potentials based on the water release curves.

Dish Assembly

Plastic petri dishes (100 by 15 mm) were filled with one of the 12 soil samples, and then a thin nonwoven veil of Kevlar (8 g m^{-2}, Fiber Glast Developments Corp., Brookville, OH) placed on top of the soil. Sixteen seeds of one of the six cultivars were positioned on top of the Kevlar veil, eight from one seed lot and eight from the other. The lid was then sealed onto the petri dish with Parafilm. This was repeated with all 12 soil samples and six cultivars. The filled dishes were placed seed-side down in large sealed plastic containers to reduce evaporation. The containers were put in a growth chamber at 20°C. The process was then repeated, but the containers were placed in another growth chamber set at 15°C. The above was then repeated two more times for a total of three replications.

Assembly of replications one and two required about 2 h each, and replication three less than 1 h, so the entire process was finished within 5 h. At 24 h intervals each dish was removed from the plastic containers and each seed scored as "germinated" or "not germinated" based on a minimum radical length of 5 mm. The dishes were returned to the plastic containers in a new, random order and returned to the growth chambers. Germination counts stopped at 25 d.

The dependent variable in this experiment was the number of days required to germinate six out of eight seeds in one half of a petri dish, which was one seed lot of one cultivar. This was called days to 75% germination. The experiment was a split plot design, with an individual petri dish being the whole plot experimental unit comparing temperature, soil, soil water content, and cultivar. The eight seeds from one of the two seed lots on one half of a petri dish were the split plot experimental unit. Since seed lots were from various sources with no common criteria, seed lots were nested within cultivar (that is, variation between seed lots is considered separately for each cultivar). Soil water content levels were nested within soil type. Statistical analysis was performed using a mixed model (SAS Glimmix, Littell et al., 2006).

RESULTS

Psychrometric measurements from the WP4 and Tru Psi instruments (Fig. 1) were similar, but not identical—even after correction to periodic readings of standards. We arbitrarily chose to use water release curves developed from WP4 data. The four soil samples taken from each soil over the course of assembly of the dishes showed that water contents did not change during the assembly process (data not shown).

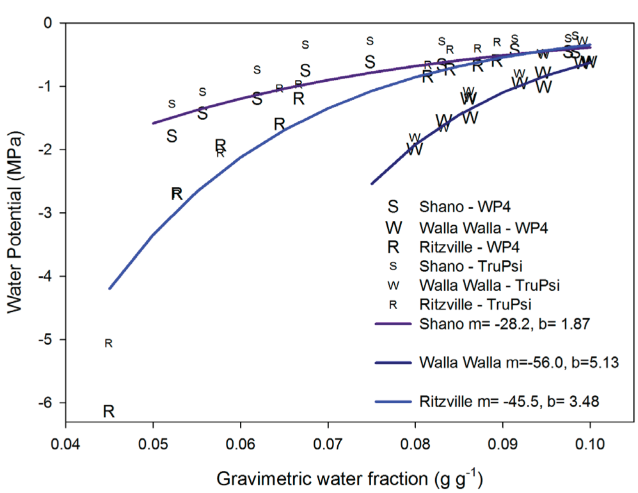

Fig. 1. Soil water release curves. Data points with large symbols were measured using a WP4 dewpoint meter. Data points with small symbols were measured using a Tru Psi thermocouple psychrometer. Coefficients are given for the curve: ln (water potential) = m × (gravimetric water fraction) + b.

We believe the germination response to the driest Shano soil at 15°C (Fig. 2) is an outlier caused by inaccuracy in the water potential curve at the dry end in this sandy soil. If we disregard this outlier, then it becomes clear soil type had no effect on rates of germination. The presentation of results will, therefore, concentrate on the water potential of the soils and not the soil types.

Statistical analysis was performed only on the eight soil water potentials where germination was completed within the measurement period. Main effects of the experimental factors and their interactions are compared in Table 1. It is well known that germination rates are affected by temperature. It is not surprising, therefore, that temperature had the largest effect on germination, with a mean of 4.78 d at 15°C, versus a mean of 3.62 d at 20°C. Water potential produced the next largest F value, followed by cultivar and seed lot differences within each cultivar. The temperature by water potential interaction was almost as large as the lot effect, but all other interactions were much smaller.

Averaged over the two temperatures, germination data indicated distinct divisions of soil water potential into three groups of four (Table 2). At potentials from -0.52 to -1.14 MPa, germination was rapid at 3 to 4 d. From -1.37 to -1.57 MPa, germination took an average of 1.3 d longer. In the driest four soils, -1.86 MPa and lower, many split plot units (eight seeds on one side of a petri dish) did not achieve the 75% germination criteria before termination of measurements on Day 25. When data from the four water potentials between -0.52 and -1.14 MPa are compared, as a group, to data associated with water potentials from -1.37 to -1.57 MPa, the 1.3 d difference is highly significant ($p > F = 0.0001$).

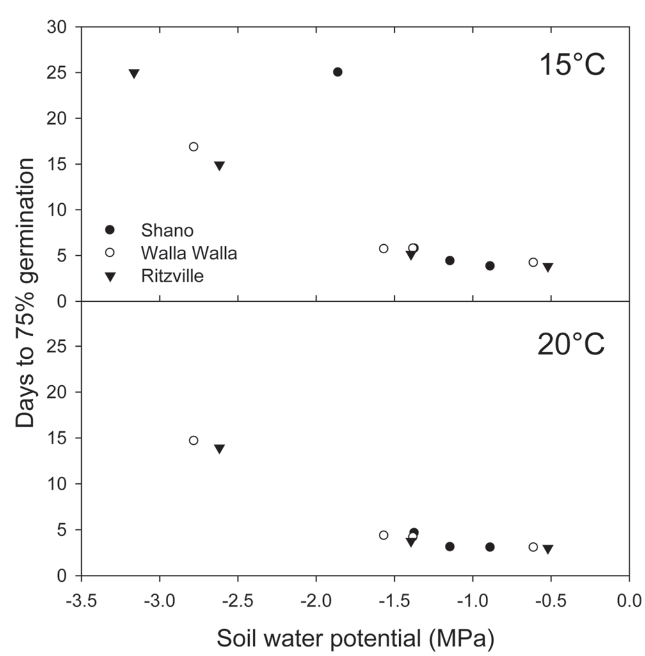

Fig. 2. Mean number of days to attain 75% germination for the three soil types, each at four different water potentials. Note that not all seed lots attained 75% germination at the four lowest water potentials (see Table 2).

Table 1. Results of a mixed model statistical analysis of data from the eight soils with high enough water potential to complete germination. The experimental factors and interactions are listed in order of the significance of their effect, as indicated by the F value. Also listed are the numerator and denominator degrees of freedom, and the probability of a greater F value.

Type III Tests of Fixed Effects				
Effect	Num DF	Den DF	F Value	Pr > F
Temperature	1	192	923.33	<0.0001
Water Potential	7	192	195.13	<0.0001
Cultivar	5	192	43.00	<0.0001
Lot(within Cultivar)	6	282	7.07	<0.0001
Temperature × Water Potential	7	192	6.23	<0.0001
Temperature × Cultivar	5	192	2.97	0.0131
Water Potential × Cultivar	35	192	2.70	<0.0001
Temperature × Water Potential × Cultivar	35	192	1.80	0.0070

Differences among cultivars are significant (p > F = 0.0001, Table 1). Lots within cultivar differed also (p > F = 0.0001). The range of cultivar differences was 0 to 0.91 d, with an average difference of 0.34 d. Lots within each cultivar differed in germination time from 0.13 to 0.33 d, with an average of 0.20 d. Since we only investigated two seed lots of each cultivar, the random selection of seed lots could have a large influence on performance attributed to cultivars. This is why a mean separation procedure was not performed for cultivar differences.

With that caution in mind, note that the cultivar Eltan stands out from the rest (Table 2). All but one experimental unit of the cultivar Eltan achieved 75% germination at -2.62 and -2.78 MPa. One lot of Stephens produced five out of six experimental units with 75% germination in these two soils but took 3 d longer than the slowest lot of Eltan. The other Stephens lot had poor success. One lot of Eltan also achieved the only success in the -1.86 and -3.16 MPa soils.

DISCUSSION

Our principal objective was to establish criteria for adequate and marginal water potentials of silt loam soils for germinating winter wheat. We used three different soils to verify our assumption that soil type would not influence the water potentials needed for germination. Figure 2 shows that the germination response was similar among the three soils, except for one outlier, the driest Shano soil. Germination in the Shano soil estimated at -1.86 MPa and the Ritzville soil estimated at -3.16 MPa are identical, with only one replication of one lot of one cultivar attaining 75% germination (Table 2), yet there were two soils, which have estimated soil water potentials drier than -1.86 MPa where substantial germination was recorded. We feel this is most likely due to inaccuracy of the water release curve for the dry end of the Shano soil. The biological response of germinating seed appears to be consistent in relation to water potential, as evidenced by consistent results between replications and within each soil batch (Fig. 2). Therefore, the Shano soil we estimated to be -1.86 MPa probably actually had a lower water potential than the soils estimated to be -2.62 and -2.78 MPa.

Two temperatures were used to represent a range of field conditions and check for cultivar or seed lot variation. Interaction effects between temperature and other variables were statistically significant but small in magnitude (Table 1). Setting aside the known effect of temperature on germination rates, water potential was the controlling factor, and rapid germination was measured down to about -1.1 MPa (Table 2). From -1.3 to about -1.6 MPa, germination was slightly slower but complete. Below -1.6 MPa, germination was incomplete.

Seed lots were random selections from available seed sources, and there was no relationship between them. Our goal in including seed lot as a factor was to guard against erroneous conclusions about cultivars when seed size, growing conditions, and storage are known to affect performance in some species. Having only two seed lots of each cultivar was enough to establish that differences between lots can be as large or larger than differences between cultivars. Even though statistical analysis of this experi-

Table 2. Time (days) for split plot experimental units (eight seeds on one side of a petri dish) to reach 75% germination. Mean of two temperatures and three replications (n = 6). Values within parenthesis in the last four rows of data indicate the number of experimental units that attained 75% germination, if less than six.

Soil (water content, g g^{-1})	Soil water potential	Bruehl		Eltan		ORCF-102		Skiles		Stephens		Tubbs 06	
		lot A	lot B	lot A	lot B	lot A	lot B	lot A	lot B	lot A	lot B	lot A	lot B
	MPa	days to 75% germination											
Ritzville (0.091)	-0.52	3.5	3.2	3.0	3.2	3.7	3.5	3.7	3.5	3.5	3.5	3.3	3.5
Walla Walla (0.100)	-0.61	3.5	3.5	3.5	3.3	3.5	3.7	4.0	3.8	3.7	3.8	3.5	3.7
Shano (0.071)	-0.89	3.5	3.2	3.2	3.0	3.5	3.5	3.7	3.7	3.5	3.5	3.5	3.5
Shano (0.062)	-1.14	3.7	3.5	3.5	3.5	3.5	4.0	4.0	4.2	3.8	4.2	3.5	3.7
Walla Walla (0.086)	-1.37	5.7	5.3	4.0	4.0	5.0	5.0	6.2	5.7	5.7	4.8	5.3	5.7
Ritzville (0.069)	-1.38	5.2	4.8	4.2	4.3	5.0	5.5	5.5	5.7	5.0	4.8	4.7	5.0
Shano (0.055)	-1.39	4.7	4.0	3.8	4.2	4.5	4.8	4.8	4.7	4.5	4.5	4.5	4.7
Walla Walla (0.084)	-1.57	5.2	4.7	3.8	4.5	4.8	5.5	5.8	5.3	5.5	5.0	4.8	5.2
Shano (0.044)	-1.86	–†	–	25 (1)	–	–	–	–	–	–	–	–	–
Ritzville (0.055)	-2.62	17.7 (3)	15 (2)	9.0	12.8 (5)	15 (4)	13 (2)	19 (3)	19.5 (2)	14 (1)	16.6 (5)	14 (2)	15.3 (4)
Walla Walla (0.073)	-2.78	18 (2)	17 (3)	9.3	13.5	18 (3)	17.8 (5)	18 (3)	18 (3)	14 (1)	16.2 (5)	21 (1)	23.7 (3)
Ritzville (0.051)	-3.16	–	–	25 (1)	–	–	–	–	–	–	–	–	–

† None of the experimental units attained 75% germination.

ment produced a highly significant cultivar effect, two seed lots of each are not sufficient to be confident which cultivars truly differ from one another.

Our results indicate that some seed lots germinate slightly faster under good soil water conditions and continue to outperform most other seed lots under extremely dry conditions (for example, both lots of Eltan and lot B of Stephens, Table 2). Clearly, any investigation of cultivar differences will need to consider seed condition and include a large population of seed sources. If a better understanding of the reason for variation among seed lots is developed, it is possible that germination under marginal conditions can be improved by altering seed condition instead of through breeding.

Germination is only the first step in establishing a crop, and agronomists will need to consider the effects of available water on root growth, leaf development, disease resistance, and general plant vigor. Our results indicate that for 12 cultivar-by-seed lot samples, quick germination of winter wheat can be expected at soil water potentials above -1.1 MPa, and slightly slower but complete germination can be expected from -1.1 down to about -1.6 MPa. As documented here and by other research, seed lots and cultivars can differ significantly in germination performance especially at marginal water contents. If improvements in germination performance at low water contents are desired, it will be important to characterize the influence of seed production and storage conditions.

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