Critical water potentials for germination of wheat cultivars in the dryland Northwest USA

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Abstract

Low soil water potential limits or prevents germination and emergence of rainfed winter wheat (*Triticum aestivum* L.). This phenomenon is particularly pronounced in the winter wheat–summer fallow region of the US Inland Pacific Northwest, where wheat is routinely sown deep to reach moisture with 12–15 cm of soil covering the seed. Wide differences in seedling emergence among winter wheat cultivars have been reported, but few previous experiments have examined germination differences among cultivars as a function of water potential. The objective of our laboratory study was to quantify seed germination of five commonly sown winter wheat cultivars (Moro, Xerpha, Eltan, Buchanan and Finley) at seven water potentials, ranging from 0 to − 1.5 MPa. Germination was measured as a function of time for a period of 30 d. At higher water potentials (0 to − 0.5 MPa), all cultivars had germination of more than 90%. At the lowest water potentials (− 1.0 to − 1.25 MPa), however, Moro consistently exceeded the other cultivars for speed and extent of germination, with total germination of 74% at − 1.0 MPa and 43% at − 1.25 MPa. Since its release in 1966, Moro has been sown by farmers when seed-zone water conditions are marginal. Scientists have long known that coleoptile length is an important factor controlling winter wheat seedling emergence from deep sowing depths. In addition to having a long coleoptile, our data suggest that Moro's known excellent emergence ability from deep sowing depths in dry soils can also be attributed to the ability to germinate at lower water potentials than other cultivars.

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Introduction

Dryland wheat farming in Mediterranean climates is heavily dependent on winter precipitation and over-winter water storage in the soil (Schillinger *et al.*, 1998; Rebetzke *et al.*, 2007). In some Mediterranean regions, the soil is left fallow for a year or more between crops to store a portion of over-winter precipitation to establish the next crop. Optimum winter wheat yield potential in the low-precipitation (< 300 mm annual) region of the Inland Pacific Northwest is achieved when winter wheat is planted into carryover water in late August–early September after a 13-month fallow. However, seed-zone water content is often marginal by this date and farmers use specially designed deep-furrow drills to place seed as deep as 12–15 cm below the soil surface, and winter wheat seedlings emerge through 12 cm or more of soil cover (Schillinger *et al.*, 1998).

Water potential and temperature are the most important factors affecting seed germination (Lindstrom *et al.*, 1976). For germination, the seed must imbibe water from the surrounding soil. Adverse effects of reduced water potential on germination and seedling growth have been reported for several crops. Low water potential decreased the percentage of germination in sorghum (*Sorghum bicolor* L.) at 25°C, from 95% at − 0.82 MPa to 72% at − 1.23 MPa (Patane *et al.*, 2009). Murungu *et al.* (2003) reported that cotton emergence decreased from 94 to 35% when the water potential was lowered from − 0.1 to − 0.5 MPa, and to only 2% at − 1.0 MPa. In sunflower (*Helianthus annuus* L.), no seed germination was observed when the water potential reached − 1.2 MPa and a 70% reduction in seed germination was observed at a water potential < − 0.6 MPa (Kaya *et al.*, 2006). For wheat, Dhanda *et al.* (2004) reported an average germination reduction of

14–65% when the water potential was reduced from 0 to −1.0 MPa.

Imbibition, the first phase in seed germination, occurs as a result of increased hydration of the seed (Hegarty, 1978). The imbibition process depends on both intrinsic properties of the seed and the availability of water in the soil (Simon, 1984; Studdert *et al.*, 1994). Soil water potential affects seed germination either directly through changes in water content and hydraulic conductivity in the soil, or indirectly through physiological processes occurring during imbibition and seed germination (Lindstrom *et al.*, 1976). In general, as the water potential is lowered below a certain threshold, germination rate and seedling growth are reduced and delayed (Lyles and Fanning, 1964). Owen (1952) reported that this threshold is −1.5 MPa for >70% of wheat germination. However, a search of the current literature reveals that, for several wheat cultivars, the critical water potential for 85% or more germination of seeds is between −0.5 and −1.0 MPa (Lindstrom *et al.*, 1976; Al-Karaki, 1998; Wuest *et al.*, 1999; Almansouri *et al.*, 2001; Rinaldi *et al.*, 2005; Murungu, 2011) as shown in Table 1. Wuest and Lutcher (2012) reported critical water potentials for 75% germination of several dryland wheat cultivars to be between −1.1 and −1.6 MPa, with some cultivars achieving 75% germination at even lower water potentials.

In laboratory studies, seed germination as a function of water potential is often tested with soil adjusted to desired water potentials or by using polyethylene glycol (PEG) solutions. Polyethylene glycol effectively lowers the water potential of an aqueous solution (Lagerwerff *et al.*, 1961; Williams and Shaykewich, 1969; Tingey and Stockwell, 1977). Large-molecular-weight (i.e. >6000 g mol^{-1}) PEG cannot penetrate cell membranes (Carpita *et al.*, 1979). Seeds are often placed on PEG-soaked filter papers (Sharma, 1973; Redmann, 1974; Wang *et al.*, 2005) or cellulose membranes in contact with PEG (Hardegree and Emmerich, 1992; Hardegree and Van Vactor, 1999), and the percentage of seeds germinated is counted at the PEG concentration corresponding to each water potential. Blum *et al.* (1980) tested the germination of ten spring wheat cultivars in a series of PEG solutions ranging in potential from −0.59 to −1.13 MPa, and found significant differences in germination percentage among cultivars.

Several calibration equations have been published that relate PEG concentration to water potential (Michel and Kaufmann, 1973; Michel, 1983; Michel *et al.*, 1983; Money, 1989). The degree of polymerization of PEG affects the relation between concentration and water potential, requiring different calibrations for different types of PEG (Money, 1989). There is also evidence that the presence of a porous matrix, such as a filter paper, will alter the water potential of a PEG solution by exclusion of the large PEG molecules from the porous matrix and up-concentration of the PEG in the solution phase (Hardegree and Emmerich, 1990). Given this influence of the filter paper or porous matrix on the effective water potential and the dependence of the water potential on the degree of polymerization, it is advisable to calibrate each PEG solution rather than to rely on a previously published calibration equation.

The objective of our research was to determine the critical water potential required for seed germination of five winter wheat cultivars commonly sown deep into dry summer-fallowed soils in the 150- to 300-mm annual precipitation region of the Inland Pacific Northwest. We consider a germination rate of >90%

Table 1. Germination of different wheat cultivars at different water potentials

Wheat cultivar	Water potential range investigated (−MPa)	Minimum potential for >85% germination (−MPa)	Temperature (°C)	Time to maximal germination (d)	Reference
McCall, Nugaines	0.04–2.0	1.0[a] 0.6[b]	25 20	20	Lindstrom *et al.* (1976)
Madsen	0.15–4.5	1.1	23–28	na	Wuest *et al.* (1999)
Omrabi-5, Belikh, Cando	0.15–1.57	0.58	24	6	Almansouri *et al.* (2001)
Simeto	0.01–0.8	0.4	25	15	Rinaldi *et al.* (2005)
Dande, Insiza, Kana, S95063	0–1.5	0.5	25	na	Murungu (2011)
Hourani-27/ACSDA-176	0–1.2	0.4	25	na	Al-Karaki (1998)
Bruehl, Eltan, ORCF-102, Skiles, Stephens, Tubbs 06	0.52–3.16	1.57[c]	15–20	na	Wuest and Lutcher (2012)

na, Not available.
[a] Under laboratory conditions.
[b] Under field conditions.
[c] Minimum potential for >75% germination (unusual long germination times are excluded from these data).

as successful germination to determine the critical water potential. We hypothesized that there are significant differences in the germination water potentials among the different cultivars, and that the cultivars having the best germination under driest conditions are also those that can emerge the best in dryland soil.

Materials and methods

Wheat cultivars

The germination of five winter wheat cultivars commonly grown in the 150- to 300-mm annual precipitation zone of the Inland Pacific Northwest (USA) was evaluated under seven water potentials. The cultivars were Moro (Rohde, 1966), Buchanan (Donaldson, 1993), Finley (Donaldson et al., 2000), Eltan (Peterson et al., 1991) and Xerpha (Jones et al., 2010). Moro is a standard height (i.e. no dwarfing genes), soft, white cultivar released 1966 but still planted today due to excellent emergence ability, despite modest grain yield potential, weak straw that causes lodging, and poor disease resistance. Buchanan and Finley are standard height, hard, red cultivars that are widely sown in the driest portion of the region that receives <225 mm annual precipitation, where winter wheat is under moderate to severe water stress for most of the growing season (Donaldson, 1996) and, therefore, produce relatively low grain yields. However, due to the water stress, farmers often achieve optimum grain protein from hard, red winter wheat with no extra nitrogen fertilizer input and the grain is worth more money for a given mass compared to soft, white winter wheat that has no protein requirement. Eltan and Xerpha are semi-dwarf soft, white cultivars that contain the Rht1 dwarfing gene to reduce plant height. Eltan and Xerpha have higher grain yield potential, but reduced emergence capability from deep sowing depths, compared to standard-height cultivars Moro, Buchanan and Finley. Seeds for the study were newly harvested (i.e. harvested the same year) from a rainfed nursery at the WSU Dryland Research Station at Lind, Washington, USA. Seeds were stored in paper bags under ambient laboratory conditions until use. Seeds were not treated with any chemical. Initial seed water content was near 9% by weight and the initial seed water potential was < −55 MPa (determined with a dew-point psychrometer, WP4, Decagon Devices, Pullman, Washington, USA).

Polyethylene glycol solutions

We used PEG (PEG-8,000, molecular weight 7000–8000 g mol^{-1}, CAS No. 5322–68-3, Fisher Scientific,

Suwanee, Georgia, USA) to prepare a series of aqueous solutions with water potentials of 0, −0.25, −0.5, −0.75, −1.0, −1.25 and −1.5 MPa. In a second set of experiments, we refined the potentials in the range between −0.5 and −1.0 MPa, and used the additional potentials of −0.65, −0.75 and −0.85 MPa.

The quantity of PEG required to obtain these specific water potentials was determined based on a calibration curve that we developed. Water potentials for the PEG solutions were measured with a dew-point psychrometer (WP4, Decagon Devices). We measured both pure solutions as well as solution-soaked filter papers (Whatman No. 1) to determine the effect of the filter paper, as suggested by Hardegree and Emmerich (1990). Two filter papers of diameter 90 mm were soaked with 4 ml of PEG solution, and equilibrated for 30 min in covered Petri dishes. A portion of filter paper was then removed and placed in the dew-point psychrometer for measurements. All measurements were obtained in a temperature-controlled laboratory at 20°C. Michel (1983) developed the following calibration equations relating PEG concentrations to water potential:

$$\psi = 0.129[PEG]^2 T - 14.0[PEG]^2 - 0.40[PEG] \quad (1)$$

and

$$\psi = 0.130[PEG]^2 T - 13.7[PEG]^2 \quad (2)$$

where ψ is the water potential of the solution (MPa), T is the temperature (°C), and [PEG] is the mass concentration of PEG in solution [g PEG (g H_2O)$^{-1}$]. Equation (1) was based on thermocouple hydrometer data, equation (2) was based on vapour pressure osmometer data (Michel, 1983). Hardegree and Emmerich (1990) reported that equation (2) should be used for predicting the water potential for filter-paper-free PEG solutions. Our measurements, however, showed considerable differences compared to equations (1) and (2); therefore, we developed our own calibration equations. Using the same functional form as in equations (1) and (2), our calibration equations at 20°C are, for filter-paper-free solutions:

$$\psi = -12.589[PEG]^2 + 1.973[PEG] \quad (3)$$

and for the PEG-soaked filter paper (Whatman No. 1):

$$\psi = -13.449[PEG]^2 + 1.484[PEG] \quad (4)$$

where ψ is the water potential of the solution (MPa) and [PEG] is the mass concentration of PEG in solution [g PEG (g H_2O)$^{-1}$]. Experimental data and fitted calibrations (equations 3 and 4) together with the previously reported equations (1) and (2) are shown in Fig. 1.
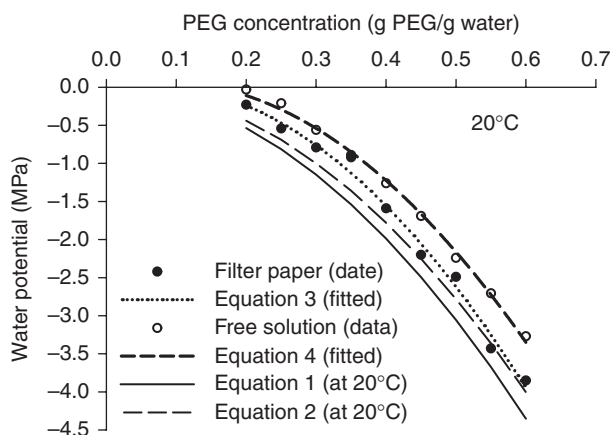
Figure 1. Calibration curves for PEG solutions with and without filter paper (two 90-mm diameter Whatman No. 1 filter papers and 4 ml PEG solution). Solid and long-dashed lines are previously published calibrations (equations 1 and 2 from Michel, 1983), short-dashed and dotted lines are our fitted curves to our experimental data (equations 3 and 4).

Germination tests

We measured the rate and extent of germination using a two-factor factorial completely randomized design with 35 treatment combinations replicated eight times. The two treatment factors were wheat cultivar (Moro, Xerpha, Eltan, Buchanan and Finley) and water potential (0, −0.25, −0.5, −0.75, −1.0, −1.25 and −1.5 MPa). Germination tests were carried out in a dark room at a controlled temperature of 20°C. Two Whatman No. 1 filter papers (90-mm diameter) were placed into 90-mm inner-diameter plastic Petri dishes. Four millilitres of the specific PEG solutions were added to each Petri dish so that the solutions completely wetted the filter paper. Twenty seeds of each cultivar were then placed on to the filter papers. This arrangement ensured that the two filter papers were completely soaked in the PEG solutions, but that the seeds were not submerged in the solution. The Petri dishes were then covered with a lid and the seam sealed with Parafilm to minimize evaporation.

We visually inspected the Petri dishes every 12 h for the first 7 d and every 24 h thereafter to count germinated seeds. Seeds were considered to have germinated when the emerging radicle had protruded 5 mm, at which point germinated seeds were removed. Observations were continued for 30 d. Every 7 d, 1 ml of PEG solution was added to Petri dishes to maintain the required water potentials.

Similar set-ups and protocols have often been used in germination experiments (Lenzi *et al.*, 1995; Tobe *et al.*, 2000; Wang *et al.*, 2005). We also used seed-free Petri dishes to verify the uniformity of the water potential during the course of the experiment. Small pieces of the filter paper were periodically removed from Petri dishes

kept at the different water potentials mentioned above, and the water potentials measured with the dew-point psychrometer. These seed-free tests showed that the water potentials remained uniform (coefficient of variation ± 7.2%) during the course of the experiments.

When seeds are placed into Petri dishes with PEG solutions, the seeds will take up water from the PEG solution and thereby cause the PEG concentration in the Petri dish to change. To quantify this effect, we monitored the change of water potential caused by the seed water uptake by measuring the water potentials as a function of time after seeds were placed into a −1.0 MPa PEG solution. These tests were done directly in the WP4 sample holders (4-cm diameter), so that the sample could be measured continuously with the dew-point psychrometer without removing the sample from the instrument. For that purpose, the amount of filter paper (4-cm diameter), PEG solution (0.87 ml), number of seeds (four) were scaled down to have the same proportions as in the larger Petri dish experiments. Measurements were done in 5- to 6-min intervals up to 100 min with a final measurement made after 24 h. After the 100-min measurement, the samples were removed from the instrument and sealed with Parafilm, and then measured again for the 24-h reading. These tests were made in duplicate with two wheat cultivars (Buchanan and Moro).

Measurement of coleoptile length

Coleoptile length measurements were obtained by growing ten seedlings of each cultivar in shallow, 20-mm-deep seed trays filled with moist vermiculite. Entries for all cultivars were replicated eight times in a completely randomized design. Seed trays were placed in a totally darkened enclosure at a constant temperature of 20°C. Coleoptile length was determined for all cultivars 7 d after planting by measuring the distance from the seed to the tip of the coleoptile for all ten seedlings in each replicate.

Data analysis

Seed germination data were analysed using analysis of variance at a confidence level of 5% with Statistical Analysis Software (SAS; SAS Institute Inc., Cary, North Carolina, USA). In addition, we calculated the median germination time and applied the hydrotime model to the data. To determine the median germination time we fitted a logistic equation (Lafond and Baker, 1986; Lafond and Fowler, 1989):

$$P_t = \frac{n_t}{N} = \frac{1}{1 + \exp(-a - b \ln t)} \tag{5}$$

where n_t is the number of seeds germinated in time t, N is the total number of seeds germinated, a and b are fitting parameters, and P_t is the ratio of number of

seeds germinated in time t and total seeds germinated. Based on equation (5), the median germination time is given as $\exp(-a/b)$ (Lafond and Baker, 1986). We used the hydrotime model as described by Bradford (1990). In brief, after Bradford (1990) the hydrotime θ_H (MPa d) is given as:

$$\theta_H = (\psi - \psi_b(g))t_g \qquad (6)$$

where ψ is the water potential (MPa), $\psi_b(g)$ is the base water potential for germination of a percentage g, and t_g is the time (d) to germinate a percentage g of seeds. For a certain seed population the hydrotime indicates how long (t_g) a seed population needs to be exposed to the water potential ψ to germinate a percentage g of seeds. Rearranging equation (6) gives:

$$\psi_b(g) = \psi - (\theta_H/t_g) \qquad (7)$$

The hydrotime θ_H is determined by linear fitting of equation (7) to probit values of the germination percentages. The fitting procedure also provides the

Table 2. Total seed germination (%) of five wheat cultivars at different water potentials. ANOVA was conducted for each day among cultivars and least-significant difference (5% LSD) values are provided

| Cultivar	Days																	
	3	4	5	6	7	8	9	10	11	12	13	14	15	20	23	25	29	30
Water Potential 0 MPa																		
Buchanan	92	94	96	97	97	nfg												
Eltan	95	98	nfg															
Finley	76	94	94	94	95	nfg												
Moro	91	98	nfg															
Xerpha	91	98	98	nfg														
LSD	11	4	ns	ns	ns													
Water Potential −0.25 MPa																		
Buchanan	2	63	92	94	94	95	95	96	nfg									
Eltan	2	68	99	nfg														
Finley	1	46	91	94	94	94	94	94	94	95	nfg							
Moro	4	67	94	98	nfg													
Xerpha	1	56	86	90	95	95	95	95	96	nfg								
LSD	ns	ns	9	6	ns	ns	ns	ns	ns	ns								
Water Potential −0.50 MPa																		
Buchanan		13	60	82	95	95	96	98	nfg									
Eltan		14	46	73	88	94	96	97	97	98	nfg							
Finley		11	44	67	86	89	91	92	nfg									
Moro		18	62	88	95	97	98	99	nfg									
Xerpha		9	41	75	92	94	94	96	96	96								
LSD		ns	17	11	5	5	5	4	ns	ns								
Water Potential −0.75 MPa																		
Buchanan		13	28	41	63	71	79	82	84	87	88	88	nfg					
Eltan		9	21	27	46	62	74	83	88	90	91	91	nfg					
Finley		3	9	16	33	54	70	76	79	81	81	81	81	83	nfg			
Moro		7	27	40	64	76	86	92	94	95	95	95	96	nfg				
Xerpha		4	15	23	44	56	73	79	82	86	86	nfg						
LSD		8	11	15	14	18	ns	16	14	13	13	11	11	ns				
Water Potential −1.0 MPa																		
Buchanan		1	3	6	17	28	35	41	43	44	44	48	48	nfg				
Eltan		1	1	6	14	24	35	41	46	51	51	56	56	59	59	nfg		
Finley		1	3	5	13	24	28	33	36	40	41	46	46	51	51	nfg		
Moro		3	16	24	38	52	59	65	68	70	70	74	74	nfg				
Xerpha		1	1	3	16	26	37	44	46	49	51	55	55	nfg				
LSD		ns	7	10	11	16	18	20	20	20	21	22	22	ns	ns			
Water Potential −1.25 MPa																		
Buchanan							0	0	3	5	7	8	8	9	9	9	nfg	
Eltan							0	0	3	6	6	8	8	nfg				
Finley							1	2	3	5	5	5	6	9	9	9	11	nfg
Moro							5	8	15	21	26	28	30	40	40	43	43	nfg
Xerpha							0	0	3	5	7	8	8	8	8	nfg		
LSD							3	5	7	9	11	11	11	12	12	11	11	

nfg, No further germination; ns, not significant.
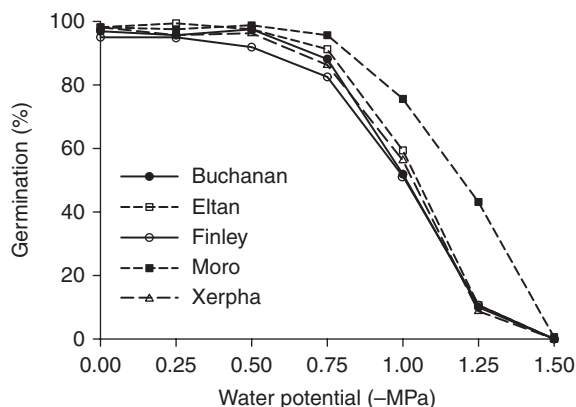
Figure 2. Total seed germination of five cultivars at seven water potentials. Symbols represent means of replicated data.

base water potentials ψ_b (g). The standard deviation of the base water potentials σ_{ψ_b} is the inverse of the slope of the fitting equation. Detailed descriptions for this approach are published elsewhere (Gummerson, 1986; Bradford, 1990). For every cultivar, we calculated the base water potential for 50% germination $\overline{\psi_b}$, the standard deviation σ_{ψ_b}, and the base water potential for 90% germination ψ_b (0.9). We applied Welchs's *t*-test for unequal sample sizes and variances (Welch, 1947) to test for differences among the cultivars at a confidence level of 5%.

Results and discussion

Dynamics of seed germination

When air-dry seeds were placed into the -1.0 MPa PEG solution, the initial reading with the dew-point psychrometer was 0.7–1.0 MPa lower than the seed-free -1.0 MPa PEG solution, indicating that the seeds were removing water vapour from the headspace in the sample holder. There was a steep gradient of the

water potential between the dry seeds (< -55 MPa) and the PEG solution (-1.0 MPa). The water potential in the sample holder then increased for the next 60 min, after which the water potential became constant. For Buchanan the constant water potential was at -1.52 ± 0.02 MPa, for Moro the constant water potential was -1.57 ± 0.04 MPa, demonstrating that the placement of dry seeds resulted in an overall decrease of the water potential inside the sample holders. We, however, consider the initial water potential to be the relevant water potential to be reported in the following, as this initial drying of the surrounding soil is also what a seed would encounter when placed into a soil at a given water potential. It is important, however, to keep in mind that the seed will dry the surrounding soil as soon as the seed is planted and imbibes water. Therefore, during the course of germination, the seed is exposed to drier conditions, and hence lower water potentials, than initially present in the seed-free soil or PEG solution.

Table 2 shows the percentage of seeds germinated for the five wheat cultivars as a function of time with seven water potentials (the -1.5 MPa data are not shown in Table 2 because there was no germination at that potential). Water potential affected both the percentage and rate of seed germination, as has been reported by others (Pawloski and Shaykewich, 1972; Lindstrom *et al.*, 1976; Lafond and Fowler, 1989; Livingston and de Jong, 1990; Wuest *et al.*, 1999). With ample water (matric potential of 0 and -0.25 MPa), more than 90% of seeds of all five cultivars germinated in <5 d. Germination was delayed as the water potential decreased.

Differences in germination among cultivars began to appear at -0.5 MPa on day 5, with Buchanan and Moro in the lead with 60 and 62%, respectively (Table 2). Moro and Buchanan also showed significantly greater germination than the other entries on day 7 and 8 at -0.75 MPa. This is especially important because -0.75 MPa is considered the lowest water potential

Table 3. Median germination time for five winter wheat cultivars at seven water potentials. ANOVA was conducted for each water potential among cultivars and least-significant difference (5% LSD) values are provided

Wheat cultivar	Water potential (MPa)							Coleoptile length (mm)
	0	-0.25	-0.5	-0.75	-1.0	-1.25	-1.5	
	--------------------------------------- days ---------------------------------------							
Buchanan	2.4	3.8	4.9	7.0	10.1	12.5	>30	88
Eltan	2.5	3.8	5.2	7.8	10.6	12.5	>30	59
Finley	2.7	4.0	5.2	8.2	10.9	13.7	>30	70
Moro	2.6	3.8	4.8	7.2	8.9	12.5	>30	94
Xerpha	2.6	3.9	5.2	8.0	10.3	11.9	>30	55
LSD	0.23	ns	0.36	0.60	1.78	ns	ns	10

Coleoptile measurements were obtained courtesy of Dr Amita Mohan, Washington State University.
ns, Not significant.

from which to expect adequate winter wheat seedling emergence through 12 cm or more soil cover (Lindstrom *et al.*, 1976; Schillinger *et al.*, 1998). At the water potential of −1.0 MPa, Moro showed significantly greater germination than all other cultivars beginning on day 7 and continuing through day 13 (Table 2). Moro continued to demonstrate the greatest germination on all days (i.e. days 9 through 29) at −1.25 MPa (Table 2). No germination for any cultivar occurred at −1.5 MPa.

Although all cultivars responded in the same general manner as water potential decreased, the quantitative magnitudes of percentage and rate of germination differed, and this is particularly evident when plotting germination as a function of water potential (Fig. 2). Germination differed among cultivars mostly at potentials between −0.75 to −1.25 MPa. Moro had the fastest rate and greatest extent of germination at water potentials of −1.0 and −1.25 MPa. The median germination times obtained by fitting equation (5) (Lafond and Baker, 1986; Lafond and Fowler, 1989) to our data are shown in Table 3. For water potentials of 0, −0.25 and −0.5 MPa, the median germination times for each cultivar were similar, but Buchanan and Moro had consistently the shortest median germination times. Clear differences were observed for the water potentials of −0.75 to −1.0 MPa, with Moro showing the shortest germination time at −1.0 MPa.

Critical water potentials for seed germination

All cultivars had <80% germination at a matric potential of −1.0 MPa, but >90% at potentials >−0.5 MPa, suggesting that the critical water potential is between −0.5 and −1.0 MPa. To pinpoint the critical water potential more accurately, we tested germination with a higher resolution of water potentials (Fig. 3). At −0.85 MPa, total seed germination was <90% for Eltan, Finley and Xerpha, but >90% for Buchanan and Moro. This suggests that the critical water potential for Eltan, Finley and Xerpha is between −0.75 and −0.85 MPa, but for Buchanan and Moro it is between −0.85 and −1.0 MPa.
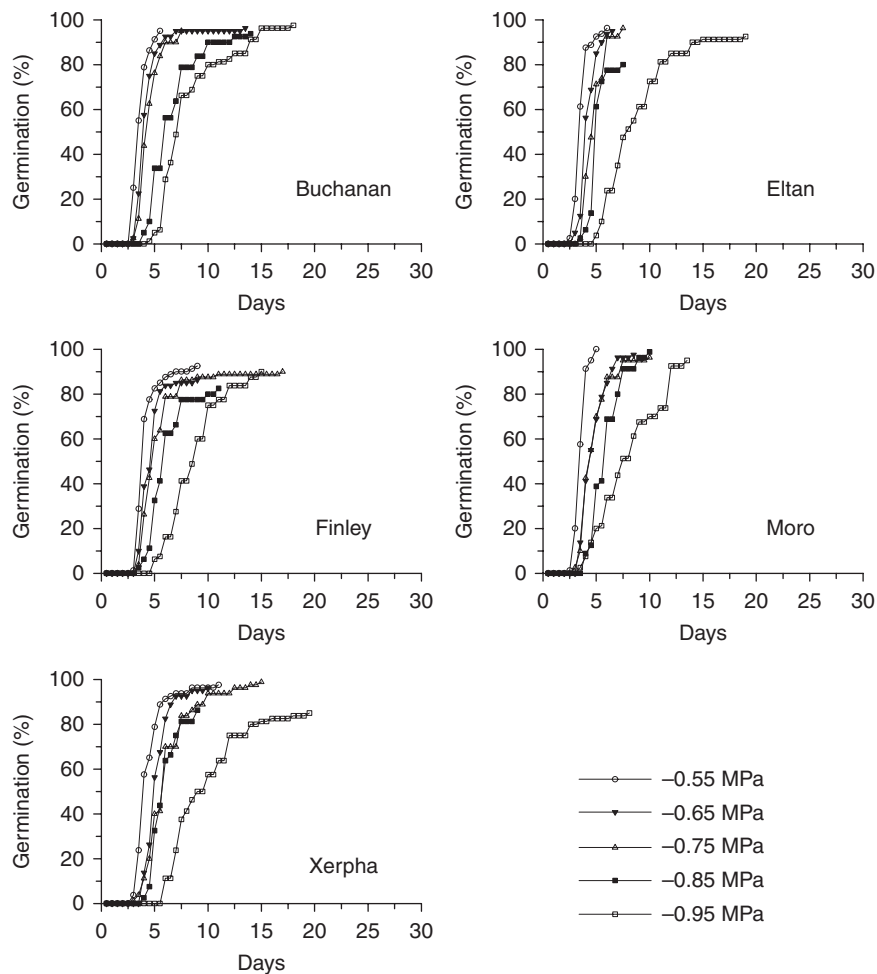

Figure 3. Seed germination of five wheat cultivars at five water potentials ranging from −0.5 to −1.0 MPa. Symbols represent means of replicated data.
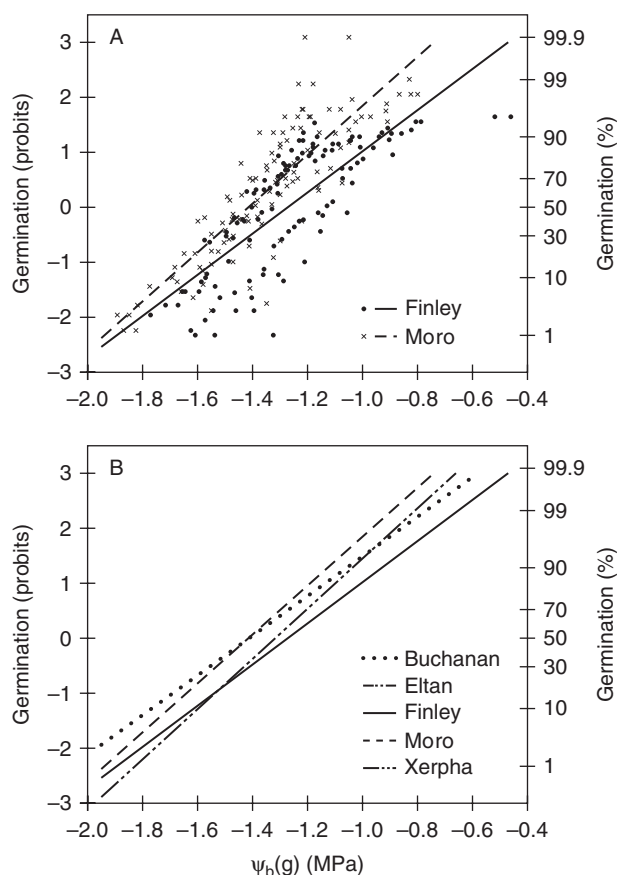
Figure 4. Results from the probit analysis. The probits of germination percentage (g) are shown as a function of the base water potential ψ_b (g). Linear regression and data points for the cultivars Finley and Moro are shown in (A). For better clarity, we only plotted the linear regression lines in (B) for all cultivars.

Figure 4A shows the probit values of the germination precentages as a function of the base water potential for the cultivars Finley and Moro. Moro germinated at higher percentages at a given water potential, indicated by the dashed line compared with the solid line in Fig. 4A. The different slopes of the fitting lines further indicate that Moro also had better germination percentages compared to Finley as the water potential increased. For better clarity, we plotted the linear regression lines only in Fig, 4B for all cultivars. Hydrotime and mean base water potentials are listed in Table 4. The mean base water potentials for 50% germination $\overline{\psi_b}$ were lowest for Moro (-1.39 MPa) and Buchanan (-1.38 MPa) followed by Xerpha (-1.30 MPa), Eltan (-1.29 MPa) and Finley (-1.27 MPa). Multiple Welch's *t*-tests among the populations resulted in no significant differences between Moro and Buchanan and no significant differences between Eltan, Finley and Xerpha. These rankings are consistent with our experimental findings described above.

The base water potential for 90% germination ψ_b (0.9) showed that Moro could germinate the best under dry conditions [ψ_b (0.9) $= -1.10$ MPa], followed by Buchanan and Xerpha [ψ_b (0.9) $= -1.02$ MPa]. There were no differences among the 90% germination base water potentials among Buchanan, Eltan and Xerpha, likely because the hydrotime model assumes a normal distribution of germination events. Our observation of germination ended after 30 d but, according to the model, germination is still likely to occur after the 30-d period. Hence, we were not able to detect all possible germination events within the time of the experiments.

Coleoptile length

Seedling emergence not only depends on germination but also on how well the emerging seedling can penetrate the overlying soil. Depth of soil covering the seed, penetration resistance, crusting of the soil surface, seedling elongation rate and coleoptile length all affect emergence (Gul and Allan, 1976; Lindstrom *et al.*, 1976; Hadas and Stibbe, 1977). Moro had a coleoptile length of 94 mm, followed by Buchanan at 88 mm, while Xerpha, Eltan and Finley had coleoptiles $\leq$70 mm in length (Table 3). The coleoptile lengths of Moro and Buchanan were significantly longer than those of the other cultivars. Previous studies showed that coleoptile length is significantly related to emergence ability from deep sowing depths, accounting for 60% of the variability among cultivars (Schillinger *et al.*, 1998).

Conclusions

Field and laboratory experiments, as well as farmers' experience, indicate that the standard-height cultivars Moro and Buchanan with long coleoptiles have superior emergence from deep sowing depths compared to semi-dwarf cultivars with shorter coleoptiles. Our data also show that Buchanan and Moro have comparatively

Table 4. Results from the hydrotime model: hydrotime θ_H, mean base water potential $\overline{\psi_b}$, standard deviation σ_{ψ_b} and base water potential for 90% germination ψ_b (0.9). Mean base water potentials followed by the same letter do not differ at $P = 0.05$

Wheat cultivar	θ_H (MPa d)	$\overline{\psi_b}$ (MPa)	σ_{ψ_b} (MPa)	ψ_b (0.9) (MPa)
Buchanan	3.49	-1.38^a	0.28	-1.02
Eltan	2.93	-1.29^b	0.22	-1.01
Finley	3.22	-1.27^b	0.27	-0.92
Moro	3.30	-1.39^a	0.22	-1.10
Xerpha	3.45	-1.30^b	0.22	-1.02

greater germination at low water potentials than other cultivars tested. More specifically, our data show that Moro winter wheat exceeded the other cultivars for germination at water potentials of −1.0 and −1.25 MPa. These results demonstrate a significant advantage of a wheat cultivar to better germinate at lower water potentials compared to other cultivars.

Farmers and scientists in the US Pacific Northwest have long known that Moro is the cultivar most capable of emerging from deep sowing depths in dry soils, and for this reason, the 47-year-old Moro continues to be planted today despite many agronomic weaknesses and relatively low grain yield potential. Our data demonstrate that, in addition to coleoptile length, the ability of the seeds to germinate at low water potentials is likely an important factor governing winter wheat seedling emergence from deep sowing depths in dry soils. Given that climate change may cause many dryland production areas to become even drier (IPPC, 2007), the ability to germinate from drier soil is likely to become even more important. Improvement of drought tolerance of crops is an important and recognized goal for plant breeding in view of climate change and continuing population increase (Godfray et al., 2010). A next logical research step will be to determine if genetic traits for germination under low water potential can be transferred into new, modern wheat lines through plant breeding.

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References

Al-Karaki, G.N. (1998) Response of wheat and barley during germination to seed osmopriming at different water potential. *Journal of Agronomy and Crop Science* **181**, 229–235.

Almansouri, M., Kinet, J.M. and Lutts, S. (2001) Effect of salt and osmotic stresses on germination in Durum wheat (*Triticum durum* Desf.). *Plant Soil* **231**, 243–254.

Blum, A., Sinmena, B. and Zev, O. (1980) An evolution of seed and seedling drought tolerance screening test in wheat. *Euphytica* **29**, 727–736.

Bradford, K.J. (1990) A water relations analysis of seed germination rates. *Plant Physiology* **94**, 840–849.

Carpita, N.C., Sabularse, D., Montezinos, D. and Delmer, D.P. (1979) Determination of the pore size of cell walls of living plant cells. *Science* **205**, 1144–1147.

Dhanda, S.S., Sethi, G.S. and Behl, R.K. (2004) Indices of drought tolerance in wheat genotypes at early stages of plant growth. *Journal of Agronomy and Crop Science* **190**, 6–12.

Donaldson, E. (1993) Registration of Buchanan wheat. *Crop Science* **33**, 878.

Donaldson, E. (1996) Crop traits for water stress tolerance. *American Journal of Alternative Agriculture* **11**, 89–94.

Donaldson, E., Sauer, B., Lyon, S.R., Morris, C.F. and Line, R.F. (2000) Registration of Finley wheat. *Crop Science* **40**, 1197–1198.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M. and Toulmin, C. (2010) Food security: The challenge to feeding 9 billion people. *Science* **327**, 812–818.

Gul, A. and Allan, R.E. (1976) Stand establishment of wheat lines under different levels of water potential. *Crop Science* **16**, 611–615.

Gummerson, R.J. (1986) The effect of constant temperatures and osmotic potentials on the germination of sugar beet. *Journal of Experimental Botany* **37**, 729–741.

Hadas, A. and Stibbe, E. (1977) Soil crusting and emergence of wheat seedlings. *Agronomy Journal* **69**, 547–550.

Hardegree, S.P. and Emmerich, W.E. (1990) Effect of polyethylene glycol exclusion on the water potential of solution-saturated filter paper. *Plant Physiology* **92**, 462–466.

Hardegree, S.P. and Emmerich, W.E. (1992) Effect of matric-priming duration and priming water potential on germination of four grasses. *Journal of Experimental Botany* **247**, 233–238.

Hardegree, S.P. and Van Vactor, S.S. (1999) Predicting germination response of four cool-season range grasses to field variable temperature regimes. *Environmental and Experimental Botany* **41**, 209–217.

Hegarty, T.W. (1978) The physiology of seed hydration and dehydration and the relation between water stress and the control of germination: A review. *Plant Cell and Environment* **1**, 101–119.

IPPC (2007) *Fourth assessment report: Climate change 2007, the AR4 synthesis report*. Geneva, Switzerland, Intergovernmental Panel on Climate Change.

Jones, S.S., Lyon, S.R., Balow, K.A., Gollnick, M.A., Murphy, K.M., Kuehner, J.S., Murray, T.D., Chen, X.M., Engle, D.A. and Campbell, K.G. (2010) Registration of Xerpha wheat. *Journal of Plant Registrations* **4**, 137–140.

Kaya, M.D., Okcu, G., Atak, M., Cikih, Y. and Kolsarici, O. (2006) Seed treatments to overcome salt and drought stress during germination in sunflower (*Helianthus annuus* L.). *European Journal of Agronomy* **24**, 291–295.

Lafond, G.P. and Baker, R.J. (1986) Effects of genotype and seed size on speed of emergence and seedling vigor in nine spring wheat cultivars. *Canadian Journal of Plant Science* **26**, 341–346.

Lafond, G.P. and Fowler, D.B. (1989) Soil temperature and water content, seeding depth, and simulated rainfall effects on winter wheat emergence. *Agronomy Journal* **81**, 609–614.

Lagerwerff, J.V., Ogata, G. and Eagle, H.E. (1961) Control of osmotic pressure of culture solutions with polyethylene glycol. *Science* **133**, 1486–1487.

Lenzi, A., Fambrini, M., Barotti, S., Pugliesi, C. and Vernieri, P. (1995) Seed germination and seedling growth in a wilty mutant of sunflower (*Helianthus annuus* L.): effect of abscisic acid and osmotic potential. *Environmental and Experimental Botany* **35**, 427–434.

Lindstrom, M.J., **Papendick, R.I. and Koehler, F.E.** (1976) A model to predict winter wheat emergence as affected by soil temperature, water potential, and depth of planting. *Agronomy Journal* **68**, 137–141.

Livingston, N.J. and de Jong, E. (1990) Matric and osmotic potential effects on seedling emergence at different temperature. *Agronomy Journal* **82**, 995–998.

Lyles, L. and Fanning, C.D. (1964) Effects of presoaking, moisture tension, and soil salinity on the emergence of grain sorghum. *Agronomy Journal* **56**, 518–520.

Michel, B.E. (1983) Evaluation of the water potentials of solutions of polyethylene glycol 8000 both in the absence and presence of other solutes. *Plant Physiology* **72**, 66–70.

Michel, B.E. and Kaufmann, M.R. (1973) The osmotic potential of polyethylene glycol 6000. *Plant Physiology* **51**, 914–916.

Michel, B.E., **Wiggins, O.K. and Outlaw, W.H. Jr** (1983) A guide to establishing water potential of aqueous two-phase solutions (polyethylene glycol plus dextran) by amendment with mannitol. *Plant Physiology* **72**, 60–65.

Money, N.P. (1989) Osmotic pressure of aqueous polyethylene glycols. *Plant Physiology* **91**, 766–769.

Murungu, F.S. (2011) Effects of seed priming and water potential on seed germination and emergence of wheat (*Triticum aestivum* L.) varieties in laboratory assays and in the field. *African Journal of Biotechnology* **10**, 4365–4371.

Murungu, F.S., **Nyamugafata, P.**, **Chiduza, C.**, **Clark, L.J. and Whalley, W.R.** (2003) Effects of seed priming, aggregate size and soil matric potential on emergence of cotton (*Gossypium hirsutum* L.) and maize (*Zea mays* L.). *Soil and Tillage Research* **74**, 161–168.

Owen, P. (1952) The relation of germination of wheat to water potential. *Journal of Experimental Botany* **31**, 188–203.

Patane, C., **Cavallaro, V. and Cosentino, S.L.** (2009) Germination and radical growth in unprimed and primed seeds of sweet sorghum as affected by reduced water potential in NaCl at different temperatures. *Industrial Crops and Products* **30**, 1–8.

Pawloski, M.C. and Shaykewich, C.F. (1972) Germination of wheat as affected by soil water stress. *Canadian Journal of Plant Science* **52**, 619–623.

Peterson, C.J., **Allan, R.E.**, **Rubenthaler, G.L. and Line, R.F.** (1991) Registration of Eltan wheat. *Crop Science* **31**, 1704.

Rebetzke, G.J., **Richards, R.A.**, **Fettell, N.A.**, **Long, M.**, **Condon, A.G.**, **Forrester, R.I. and Botwright, T.L.** (2007) Genotypic increases in coleoptile length improves stand establishment, vigour and grain yield of deep-sown wheat. *Field Crop Research* **100**, 10–23.

Redmann, R.E. (1974) Osmotic and specific ion effects on the germination of alfalfa. *Canadian Journal of Botany* **52**, 803–808.

Rinaldi, M., **Paolo, E.D.**, **Richter, G.M. and Rayne, R.W.** (2005) Modelling the effect of soil moisture on germination and emergence of wheat and sugar beet with the minimum number of parameters. *Annals of Applied Biology* **147**, 69–80.

Rohde, C.R. (1966) Registration of Moro wheat. *Crop Science* **6**, 502.

Schillinger, W.F., **Donaldson, E.**, **Allan, R.E. and Jones, S.S.** (1998) Winter wheat seeding emergence from deep sowing depth. *Agronomy Journal* **90**, 582–586.

Sharma, M.L. (1973) Simulation of drought and its effect on germination of five pasture species. *Agronomy Journal* **65**, 982–987.

Simon, E. (1984) Early events in germination. pp. 77–115 *in* Murray, D. (Ed.) *Seed physiology, Vol. 2, Germination and reserve mobilization*. Orlando, FL, Academic Press.

Studdert, G.A., **Wilhelm, W.W. and Power, J.F.** (1994) Imbibition response of winter wheat to water-filled pore space. *Agronomy Journal* **86**, 995–1000.

Tingey, D.T. and Stockwell, C. (1977) Semipermeable membrane system for subjecting plants to water stress. *Plant Physiology* **60**, 58–60.

Tobe, K., **Li, X. and Omasa, K.** (2000) Seed germination and radicle growth of a halophyte, *Kalidium caspicum* (Chenopodiaceae). *Annals of Botany* **85**, 391–396.

Wang, R., **Bai, Y. and Tanino, K.** (2005) Germination of winterfat (*Eurotia lanata* (Pursh) Moq.) seeds at reduced water potentials: testing assumptions of hydrothermal time model. *Environmental and Experimental Botany* **53**, 49–63.

Welch, B.L. (1947) The generalization of students problem when several different population variances are involved. *Biometrika* **34**, 28–35.

Williams, J. and Shaykewich, C.F. (1969) An evaluation of polyethylene glycol PEG 6000 and PEG 20,000 in the osmotic control of soil water matric potential. *Canadian Journal of Soil Science* **49**, 397–401.

Wuest, S.B. and Lutcher, L.K. (2012) Soil water potential requirement for germination of winter wheat. *Soil Science Society of America Journal* **77**, 279–283.

Wuest, S.B., **Albrecht, S.L. and Skirvin, K.W.** (1999) Vapor transport vs. seed-soil contact in wheat germination. *Agronomy Journal* **91**, 783–787.