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Vapor Transport vs. Seed–Soil Contact in Wheat Germination

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ABSTRACT

The assumption that seed–soil contact is important for germination of seeds has influenced imbibition research and equipment design but has not been tested. This study compared germination with and without seed–soil contact. Over a temperature range from 3 to 28°C, wheat (*Triticum aestivum* L.) seed was either provided with good seed–soil contact or separated from soil by fiberglass cloth. The germination system was sealed to prevent evaporation. At soil water potentials of −4.5 and −2.3 MPa, no seeds germinated in either treatment. When the soil water potential was −1.1 to −0.15 MPa, the average increase in germination time due to the absence of seed–soil contact was 0.3 d (5.6%). Days to germination ranged from 1.1 d at −0.15 MPa and 28°C, to 18.3 d at −1.1 MPa and 3°C. These results show that vapor transport may be the most important mechanism for imbibition and that liquid transport through seed–soil contact may make little contribution. Recognition of vapor transport as a sufficient, and perhaps dominant, mechanism for water transport between seed and soil should improve modeling efforts and planting equipment designs.

THE FLOW OF LIQUID WATER via seed–soil contact has been assumed the most important source of water for imbibing seeds. Drill designs and germination models emphasize seed–soil contact and soil moisture as critical to rapid germination. Studies conducted to develop germination models usually find a good correlation between soil moisture and germination. The actual differences in time to germination or emergence, however, vary little over a large range in matric potential or hydraulic conductivity. Changes in hydraulic conductivity of several orders of magnitude and liquid contact areas ranging from 7 to 100% sometimes result in no change in germination time (Hadas and Russo, 1974). Collins et al. (1984) found that a threefold increase in hydraulic conductivity did not significantly change water uptake by maize (*Zea mays* L.) seeds. Lafond and Fowler (1989) measured emergence times at soil water potentials ranging from −0.03 to −1.5 MPa. Time to emergence increased by only 10% at 5 to 15°C, and by 30% at 20 to 30°C. Their results are similar to those of Lindstrom et al. (1976).

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Choudhary and Baker (1982) concluded that the difference in performance of drills under certain conditions should be attributed to differences in vapor loss from the seed zone. Others have observed that low relative humidity counteracts the effectiveness of seed–soil contact (Harper and Benton, 1966), or that protection from drying is a major cause of differences in germination (Harper et al., 1965). After studying soil textures, soil water potentials, bulk density, and soil contact area, Rogers and Dubetz (1980) concluded that vapor transport might be a more important factor in the germination of wheat than previously thought. In this and all of the previously mentioned laboratory studies, vapor loss was controlled in order to maintain soil moisture at predetermined levels. At water potentials above −1.0 MPa, equilibrium vapor levels are very close to 100% relative humidity (Papendick and Campbell, 1981).

It has been proven that vapor is sufficient to germinate and grow seedlings. Owen (1952) used vapor in equilibrium with salt solutions to control the water potential of wheat seed. More than 70% of the wheat seed germinated when the relative humidity around the seed was >98.5%, which is vapor in equilibrium with water potentials greater than approximately −2.0 MPa. Despite these facts, vapor seems to have been overlooked as a factor contributing to or possibly dominating imbibition.

Bouaziz and Bruckler (1989) measured imbibition and germination rates in wheat using liquid, vapor, and combined liquid and vapor. They concluded that water potentials above −0.9 MPa are not substantially different in influencing imbibition, and that imbibition via vapor is sufficient in itself, although somewhat slower. They did not specify the distance from the seed to the vapor-supplying liquid. Collis-George and Melville (1978) measured imbibition by wheat under purely vapor transport, and found that distance from the liquid surface was a factor in imbibition rates. If the distance between the liquid surface and the seed surface influences both imbibition rates and final moisture content of seed, then studies of vapor imbibition will give very different results, depending on the methods used.

Our conclusions from examination of the literature are that seed–soil contact should not be assumed to be the primary mechanism for transport of water from soil

to seed. In soil with a water potential above approximately −0.9 MPa, relative humidity around the seed will be 99% or greater, unless vapor is escaping at a faster rate than can be supplied by the soil. Imbibition and germination can, therefore, occur in the absence of seed–soil contact. Furthermore, seed planted in soil will have extremely short distances between liquid water films and the seed surface. This study measured time to germination for wheat seeds placed in intimate seed–soil contact compared with those dependent on vapor transport alone. If liquid water transport to seed is much faster and more important for imbibition than vapor transport, then seed that lacks good seed–soil contact should be substantially delayed in germination. Our hypothesis is that seeds supplied with only water vapor will germinate almost as rapidly as seeds supplied with seed–soil contact in addition to water vapor. The difference in time to germination can be used to measure the relative contribution of the two water transport mechanisms.

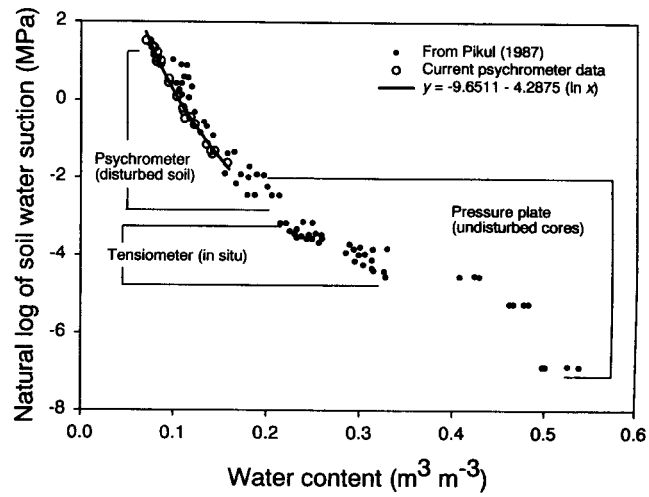

Fig. 1. Soil water potential vs. water content for Walla Walla silt loam topsoil. Psychrometer measurements and regression from this experiment are plotted with data (from Pikul, 1987) generated using the three methods indicated.

MATERIALS AND METHODS

In preliminary work, we moistened soil with a strong solution of blue or orange food coloring to a greater water potential than used in the experiment. We found that a layer of fiberglass cloth (700 × 700 yarns m^{-2}, plain weave, 190 g m^{-2}, 0.2 mm thick) acts as a barrier to liquid flow between the soil and seeds placed on top of the fiberglass. In fact, the fiberglass is hydrophobic and becomes colored by aqueous dye solution only when the solution is conducted between fibers through capillary action. This sometimes happened if a bead of solution was placed on the end of a fiber bundle, but never when the fabric was placed flat on a soil under significant negative water potential. The only way that seeds can imbibe soil moisture when separated from the soil by a layer of fiberglass cloth is through the flow of vapor or by condensation of vapor on a surface contacting the seed.

Six quantities of Walla Walla silt loam topsoil (coarse-silty, mixed, mesic Typic Haploxeroll) were brought to 0.074, 0.087, 0.102, 0.120, 0.141, and 0.165 kg kg^{-1} water content, screened through a mesh with 2.4-mm openings, sealed in plastic bags, and allowed to equilibrate for several days at 21°C. These moisture levels represent −4.5, −2.3, −1.1, −0.57, −0.29, and −0.15 MPa water potential (at bulk density of 1.0 Mg m^{-3}) as determined by a soil water release curve. The soil water release curve was generated from 32 samples of soil using a Peltier thermocouple psychrometer (Tru Psi, Decagon Devices, Pullman, WA). Extrapolation beyond the psychrometer's optimum range of measurement (−0.3 to −3.5 MPa) was justified by the general agreement with a curve generated by Pikul (1987) (Fig. 1). Within the range of moistures used in this experiment, water potential was not sensitive to bulk density.

Following a method described by Etherington and Evans (1986), the soil was packed into 90-mm diameter plastic petri dishes to a density of 1.0 Mg m^{-3} (SD = 0.04, n = 10). The first and last plates packed were used to verify soil moisture and bulk density. Treatments were then assigned randomly to the remaining 48 dishes of each soil moisture. In half of the dishes, 10 soft white wheat seeds (cv. Madsen) were pressed brush-end-first into the soil, so that only the germ end protruded slightly above the surface. In the other half, we laid a single layer of fiberglass on the soil before laying 10 seeds (crease side down) on the fiberglass. We sealed lids on the petri dishes with two to three layers of Parafilm M (American National Can Co., Chicago, IL). This procedure held the seed in the soil or against the fiberglass without inhibiting swelling of the seed. We inverted the petri dishes, so that the radicle would grow toward the lid and be easily observed.

Four replicate dishes for each of the six soil moisture levels and two seed–soil contact treatments (with or without fiberglass between the seeds and the soil) were placed in six sealed plastic boxes. Each box was placed into one of six controlled-temperature chambers, which were set at 3, 8, 13, 18, 23, or 28°C. Each box contained a recording thermometer. The plastic box reduced any water loss that might have occurred through the Parafilm.

We checked the dishes for germination every 12 h for the first 2 d and daily thereafter. Seeds were considered germinated when the length of the radicle or any other seminal root was ≥1 mm. We randomized the placement of petri dishes in the box after each germination count.

The seed was treated with difenoconazole {1-(2-[4-(chlorophenoxy)-2-chlorophenyl-(4-methyl-1,3-dioxolan-2-yl)-methyl])-1*H*-1,2,4-triazole}, metalaxyl [*N*-(2,6-dimethylphenyl)-*N*-(methoxyacetyl)-alanine methyl ester], and lindane (γ-isomer of 1,2,3,4,5,6-hexachlorocyclohexane). The seed had been stored in a sealed desiccator over a saturated solution of potassium acetate, which produces a relative humidity of 23.9% at 20°C and a seed moisture content of about 0.08 kg kg^{-1} dry mass. The six bags of soil were held at 20°C before the petri dishes were prepared and the dishes remained at 20°C until after the seeds were placed into the dishes. This was necessary to prevent condensation of moisture on the petri dish lids. Etherington and Evans (1986) measured no build-up of ethylene and only minor elevation of CO_2 in the soil-filled petri dishes. We observed that seedlings allowed to continue growing in the sealed petri dishes at room temperature for several weeks had vigorous root and shoot growth, with no apparent abnormality.

Analysis

No germination occurred at the −4.5 and −2.3 MPa soil water potentials. Seeds at these soil moistures eventually became infected by fungi. These treatments were deleted from the statistical analysis. Analysis of variance was used to determine statistical significance of the two seed–soil contact treat-

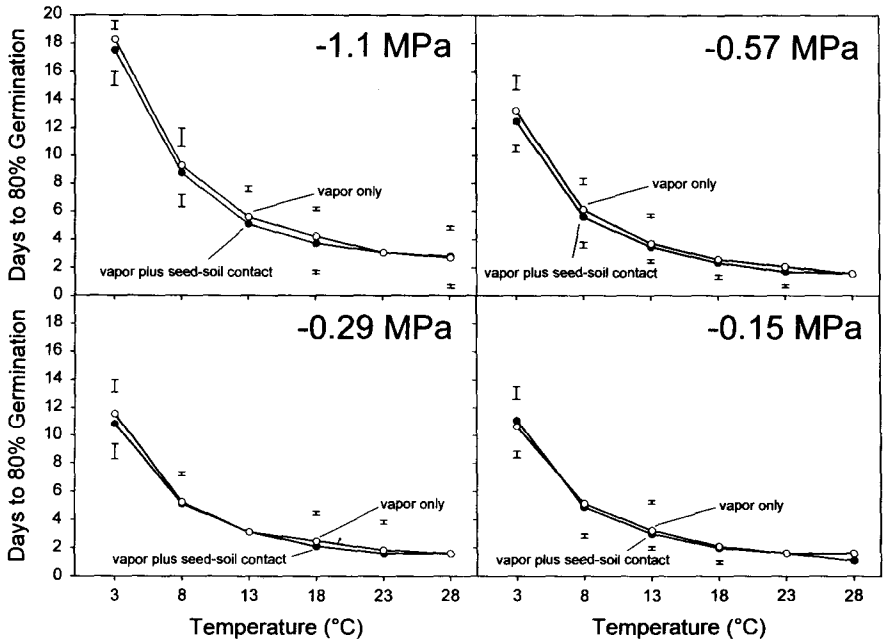

Fig. 2. Number of days required for 80% germination of wheat seeds placed in contact with soil (vapor plus seed–soil: solid symbols) or separated from soil by fiberglass cloth (vapor only: open symbols) at four soil water potentials (−1.1, −0.57, −0.29, and −0.15 MPa) and six temperatures (3, 8, 13, 18, 23, and 28°C). Error bars show standard error of the mean.

ments, the remaining four soil water potentials, and the six temperatures, with four replicates each. Percent germination was calculated as the number of germinated seeds in a dish divided by 10 (i.e., by the total number of seeds), then multiplied by 100. Number of days to 80% germination was chosen for the presentation of data, although days to 50, 70, and 90% germination produced almost identical statistical significances. The 80% germination data were slightly less variable than the 90% germination data and eliminated the need to consider the effect of nonviable seeds. Growing degree days were calculated as the temperature (°C) multiplied by days.

RESULTS

Condensation of water vapor on the lids of the sealed petri dishes was rare, and did not appear in any way to affect germination. In no instance were beads or films of water touching the wheat seeds in the dishes containing fiberglass.

All of the main effects (presence or absence of seed–soil contact; temperature; and moisture) were highly significant ($P < 0.0001$). There was no interaction between the seed–soil contact treatment and the moisture or temperature treatments. When wheat seed imbibed water through vapor alone, germination was delayed by an average of only 0.3 d (6.5 h) compared with treatments where seeds could imbibe through direct contact with soil as well as vapor (Fig. 2).

The most rapid germination occurred in 1.1 d (time to 80% germination, average of four replicates) at −0.15 MPa, 28°C, with seed–soil contact. This was the treatment with the highest temperature and moisture. The average delay in germination due to absence of seed–soil contact at 23 and 28°C temperatures for all moistures was 0.125 d (3 h).

The slowest time to 80% germination was 18.3 d for −1.1 MPa, 3°C, without seed–soil contact. Excluding the −2.3 and −4.5 MPa treatments, where no seeds germinated, this was the driest, coldest treatment. At this temperature and moisture, the difference in germination between vapor transport plus seed–soil contact vs. vapor transport alone was 0.8 d (19.2 h).

Temperature and Moisture

Temperature and moisture affected time to germination ($P < 0.0001$). A significant interaction between temperature and moisture was confined to the coldest and driest treatments. At the −1.1 MPa water potential and 28°C, germination took 2 d longer than for the three greater soil moistures; this delay increased to 6 d at 3°C. At the three soil water potentials above −1.1 MPa, days to 80% germination were essentially equal at a given temperature.

The treatments allow examination of an interesting phenomenon not related to the experimental objectives. Plant growth modelers use growing degree days to relate plant development response to time and temperature. Plotting the dependent variable as growing degree days to 80% germination rather than days shows how the driest and coldest treatments affected germination at a physiological level (Fig. 3). At the driest soil moisture producing germination (−1.1 MPa) and the coldest temperature (3°C), the relatively constant relationship between growing degree days and germination was changed significantly. The temperature and moisture data presented here agree with Blackshaw (1991), Lafond and Fowler (1989), and Lindstrom et al. (1976).

DISCUSSION

Seed–soil contact had very little effect on time to germination. The precision in this experiment allowed

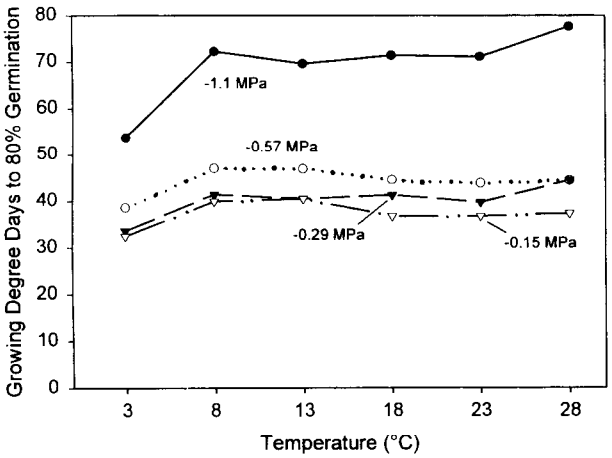

Fig. 3. Effect of temperature and soil water potential on growing degree days (base = 0°C) required for 80% germination of wheat seed.

detection of a statistically significant difference; however, the difference amounted to only 0.3 d, or a 5.6% increase in time to germination. It appears that seed–soil contact, throughout the −0.15 to −4.5 MPa soil water potential range, made very little contribution to imbibition.

It should be noted that in this experiment the arrangement of fiberglass between the seed and the soil increased the distance that vapor would have to travel from the soil surface to the seed surface. In addition, only one side of the seed was facing the fiberglass-covered soil; the other side faced the petri dish lid. In contrast, the seed in the treatment with seed–soil contact was surrounded by soil except for the embryo end. We believe, therefore, that these data overestimate the difference in time to germination with and without seed–soil contact. It is probable that an experimental method that prevents seed–soil contact while providing a much closer seed–soil distance would measure an even smaller delay in germination due to absence of seed–soil contact, indicating an even smaller role of liquid transport in the germination process.

This experiment modeled a planting system where seed is placed into disturbed soil. This is typical where fertilizer is placed below the seed, or when seeding into tilled ground, or where loosened soil is allowed to fall between the freshly opened furrow and the seed. We would expect that seed in intimate contact with moist, undisturbed soil might undergo faster imbibition rates because of the greater hydraulic conductivity of consolidated soil. In reality, however, seed placed in good contact with completely undisturbed soil is likely to be rare.

This experiment eliminated evaporation as a factor. It is possible that the relative contribution of liquid flow from soil to seed would be greater if evaporation were occurring, but evaporation would also have a negative effect on the magnitude of water films. Baker et al. (1996) reviewed the relationship of different drill designs, seed–soil contact, and evaporation.

Diurnal fluctuations in temperature and soil moisture found in actual seedbeds were not present in our experimental system. These fluctuations could cause a brief lag while relative humidity adjusts to an increase in temperature. While imbibition may slow or stop when relative humidity is at a minimum, it would resume during the phase of the daily cycle when the temperature is decreasing and vapor is condensing.

There is a pervasive assumption among agriculturalists and scientists alike that vapor transport provides very slow and perhaps inadequate levels of water for imbibition. The assumption that liquid transport is the dominant process has influenced research in the area of imbibition and also in the design of seeding equipment. In the light of the results of this experiment and review of literature, the concept of seed–soil contact should be reevaluated. We may find that the actual contact area between seed and soil water films is very small under normal conditions, and that water vapor can travel the short distances from soil water films to the seed rapidly. Measurements of seed–soil contact area and hydraulic properties of the seed surface should be corrected for vapor transport if the possibility of vapor transport is not eliminated in the measurement process.

In terms of practical application of these findings, planting equipment that does a good job of controlling loss of vapor from the seed zone should perform well under a range of moisture conditions, even if the seed is not placed in intimate contact with soil. Recognition of this fact may lead to seed placement equipment that produces less soil disruption and less compaction around the emerging seedling, or that incorporates other advantageous changes.

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