


germination

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).

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 below −0.1 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.

**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 x 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 phenoxy-2-chlorophenyl-(4-methyl-1,3-dioxolan-2-yl)- methylene-1H-1,2,4-triazole), metalaxyl [N-(2,6-dimethylphenyl)-N-(methoxyacetyl)-alanine methyl ester], and lindane (\(\gamma\)-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.

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 \(\geq 1\) mm. We randomized the placement of petri dishes in the box after each germination count.

The seed was treated with difenoconazole \[\{1-(2-[4-(chloro-phenoxyl]-2-chlorophenyl)-(4-methyl-1,3-dioxolan-2-yl)methyl]-1H-1,2,4-triazole\}, metalaxyl \[N-(2,6-dimethylphenyl)-N-(methoxyacetyl)-alanine methyl ester\], and lindane (\(\gamma\)-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-
ments, the remaining four soil water potentials, and the six
temperatures, with four replicates each. Percent germina-
tion 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 con-
taining 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 be-
tween 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 treat-
ments 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 treat-
ment 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 germi-
nation 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 germina-
tion (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 temper-
ture (3°C), the relatively constant relationship be-
tween growing degree days and germination was
changed significantly. The temperature and moisture
data presented here agree with Blackshaw (1991), La-
fond 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
mental 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 agriculturists 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.

REFERENCES

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FORAGE & GRAZING MANAGEMENT

Response of Selected and Unselected Bahiagrass Populations to Defoliation
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ABSTRACT

Recurrent restricted phenotypic selection (RRPS) has increased spaced-plant yield of ‘Pensacola’ bahiagrass (Paspalum notatum Flügge var. saurea Parodi) and led to higher-yielding, more erect genotypes. Response to defoliation was examined in three entries: selection Cycle 0, Pensacola; Cycle 9, ‘Tifton 9’, and Cycle 14. In a 3-yr plot study, two cutting heights (15 or 100 mm) in combination with three regrowth intervals (2, 4, or 8 wk) were imposed throughout 24 wk. A split-split plot arrangement of regrowth interval (whole plot), cutting height (subplot) and entry (sub-subplot) was used, with six replications. In a 2-yr grazing study, response of the same entries to defoliation from continuous stocking was evaluated. In the plot study, yield (7030 kg ha⁻¹) was maximized by low cutting height and 8-wk regrowth interval during the first year. In Year 2, a 4-wk regrowth interval and low cutting height produced the highest yield (11 220 kg ha⁻¹). Mean yields of Tifton 9 (7650 kg ha⁻¹) and RRPS cycle 14 (7320 kg ha⁻¹) were greater than Pensacola (6500 kg ha⁻¹), but response of entries to cutting height and regrowth interval varied among years. In the grazing study, herbage mass was greater for Tifton 9 (1670 kg ha⁻¹) than for RRPS (1420 kg ha⁻¹) and RRPS Cycle 14 (2000 kg ha⁻¹) than for Pensacola (1420 kg ha⁻¹). Carrying capacity of Tifton 9 (935 d ha⁻¹) was greater than Pensacola (855 d ha⁻¹). Daily gains were similar (0.34 kg) for all germplasms. Bahiagrass stand declined rapidly for RRPS Cycle 14. Continuous stocking at high grazing pressure was not suitable for RRPS Cycle 14.

Pensacola bahiagrass, a warm-season perennial introduced from South America (Burton, 1967), is an important forage in the southeastern USA and is grown on more than 2 million ha of land (Beaty and Powell, 1978). Bahiagrass is widely adapted, especially to sandy soils, and tolerates low fertility, drought, intermittent flooding, and heavy, continuous grazing. Pensacola, the earliest introduction recognized as a cultivar, is most widespread. Additional plant introductions, leading to release of ‘Argentine’ and ‘Paraguay-22,’ have historically provided germplasm alternatives.

Beginning in 1960, Burton (1974, 1982) used modified mass selection, termed recurrent restricted phenotypic selection, to develop improved bahiagrass populations from Pensacola. Werner and Burton (1991) documented the progressive morphological modifications that accompanied selection for increased aboveground yield: spaced plants of advanced populations were taller, with longer and wider leaves, but had decreased plant diameter. Morphological observations suggested that the large investment of biomass in surface energy storage structures [referred to as either rhizomes (Hitchcock, 1935; Pedreira and Brown, 1996a, 1996b; Ball et al., 1996) or stolons (Beaty et al., 1977; Sampaio et al., 1976)] that is typical of Pensacola might have been reduced by selection for more upright growth. Pedreira and Brown (1996a) confirmed that individual plants from selected populations had a higher ratio of height to diameter and fewer rhizomes. Placement at the soil surface protects stolons, which accumulate carbohydrate, from removal by cutting or grazing (Adjie et al., 1988). Pedreira and Brown (1996a) found no differences in growth rate or leaf photosynthesis among bahiagrass populations. In additional experiments, Pedreira and Brown (1996b) found lower yields of Pensacola compared with Tifton 9 and RRPS Cycle 14 in the final 2 yr of a 3-yr clipping study. Cutting at 3.5 cm resulted in harvest of a greater fraction of the total biomass than cutting at 10 cm for all populations. Response to simultaneous variation in cutting height and duration of regrowth among bahiagrass populations has not been reported. Given the dissimilar effects of mechanical harvest and grazing on plant yield and persistence (Trlica and Rittenhouse, 1993), information about the response of selected populations to grazing is needed. Our objectives were to compare the productivity and persistence of two bahiagrass populations selected for greater harvestable herbage production (Tifton 9 and RRPS Cycle 14) with the unselected population, Pensacola, under mechanical

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Abbreviations: DM, dry matter; IVDMD, in vitro dry matter disappearance; RRPS, recurrent restricted phenotypic selection.