Factors Affecting Successful Establishment of Aerially Seeded Winter Rye

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ABSTRACT
Establishing cover crops in a corn (Zea mays L.)–soybean (Glycine max L.) rotation in northern climates can be difficult due to the short time between harvest and freezing temperatures. Aerial seeding into standing crops is one way to increase the time for germination and growth. Field studies were conducted to characterize the physical and chemical properties that affect winter rye (Secale cereale L.) establishment in corn and soybean, while a germination experiment was designed to determine optimal temperature and surface soil moisture content needed for successful germination. In the field study, 31 field-scale sites (22 corn and nine soybean) were aerially seeded in southeastern Minnesota during late August to early September 2009, 2010, and 2011. Aboveground biomass was collected before the ground froze, and multiple regression analysis was used to relate biomass to multiple soil and weather conditions. Total N uptake also was determined. Overall, precipitation the week after seeding was the most important factor in determining rye establishment, although our model accounted for only 43% of the variation in biomass. The germination study characterized winter rye germination on the surface of three different soils equilibrated to –50, –200, and –500 kPa water potential placed in three low-temperature incubators at 10, 18, and 25°C. Total germination was decreased by decreasing water potential in the sandy loam but not the clay or silt loam, suggesting that moisture content may be more important than water potential at the soil surface. Generally, germination was drastically reduced below a moisture content of 0.083 g g⁻¹.

During the last quarter of the 20th century, a 2-yr corn–soybean rotation became the dominant agricultural land use in the Upper Midwest (Randall, 2003; Karlen, 2004). Recent research has shown that this agronomic practice can degrade soil quality (Karlen et al., 2006) and contribute to significant losses of NO₃ to ground and surface waters (Dinnes et al., 2002; Oquist et al., 2007). One mitigation strategy to maintain soil quality and reduce NO₃ loss is to incorporate cover crops into the rotation, which can increase the amount of time the land is covered in growing vegetation. Cereal rye is especially effective at reducing NO₃ leaching (Ditsch et al., 1993; McCracken et al., 1994; Strock et al., 2004; Fisher et al., 2011). Furthermore, rye has many other advantages, such as adding soil organic matter (Kuo and Jellum, 2002) and erosion control (Langdale et al., 1991; Kaspar et al., 2001). Additionally, rye residues suppress weeds in the spring when used as a mulch (Barnes and Putnam, 1983; Leibl et al., 1992; Dhima et al., 2006).

The benefits of cover crops have been known for many years (Odland and Knoblauch, 1938; Beale et al., 1955), although adoption has been minimal. For example, Singer et al. (2007) estimated that only 18% of farmers in the U.S. Corn Belt had used cover crops in the past. Two obstacles to adoption are the lack of knowledge about the practice and concern about various risks, particularly reports of rye negatively affecting subsequent crops. Johnson et al. (1998) reported that in Iowa, corn yields were reduced following winter rye but not after oat (Avena sativa L.). Tollenaar et al. (1993) suggested that winter rye caused a delay in corn development and a yield loss in the subsequent harvest. In both studies, the researchers hypothesized that allelopathy from the rye may have played a role in yield reductions. Researchers in Illinois found that soybean yields were reduced due to low soybean stand when rye was killed immediately before planting (Leibl et al., 1992).

In contrast, corn yields were actually improved with cover cropping compared with yields without a previous rye cover crop (Ball-Coelho and Roy, 1997; Ball-Coelho et al., 2005). Certain management practices can reduce the yield losses of corn and soybean following winter rye. Ritter et al. (1998) and Andraski and Bundy (2005) concluded that rye cover crops grown on loamy sand will not reduce subsequent corn yields if irrigation is used. Additionally, soybean and corn yields after winter rye were not reduced when the rye was killed one or more weeks before planting (Leibl et al., 1992; Strock et al., 2004; Ball-Coelho et al., 2005; Duiker and Curran, 2005; Krueger et al., 2011).

There are also uncertainties about the additional costs associated with planting and killing a secondary crop. In Minnesota and Missouri, soybean yields following a rye cover crop were comparable to yields following winter fallow, but overall economic returns were usually reduced with the cover crop (Reddy, 2001; De Bruin et al., 2005). One avenue to increase cover crop adoption is thus through cost sharing in conservation programs. While


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Abbreviations: DAS, days after seeding; GDD, growing degree days; TG50, time to 50% germination.
only 18% of survey respondents in the U.S. Corn Belt reported the use of cover crops, more than half indicated that cost sharing would increase their use of the practice (Singer et al., 2007).

In addition to previously mentioned concerns, winter cover crops can be difficult to establish in the Upper Midwest due to cool temperatures and unpredictable rainfall. Cereal rye is considered a good cover crop for cooler climates because it is cold tolerant and easy to establish (Dabney et al., 2001), but a winter cover crop meta-analysis found that grass cover crops in the north-central United States would provide only marginal environmental benefits due to the short growing season (Miguez and Bollero, 2005). Strock et al. (2004) suggested that based on average weather patterns, rye would be a successful cover crop in southwestern Minnesota in only 1 out of 4 yr. In these studies, however, rye was planted after the preceding crop was harvested, when day lengths were short and temperatures were cool. Broadcasting seed into a standing crop can result in earlier establishment than drilling the seed after harvest (Frye et al., 1988), and Feyereisen et al. (2006) predicted the greatest NO$_3$ scavenging by rye when seeded before 15 September in southwestern Minnesota. Recent research has tested these strategies by aerially seeding rye during the early fall into a standing corn or soybean crop. Preliminary unpublished data (2008) have shown promising results, but field management of this practice needs to be refined. For instance, beyond anecdotal evidence, factors that affect germination and survival of seed broadcast onto the soil surface have not been characterized.

It has been well documented that adequate soil moisture is required for optimal seed germination (Bewely and Black, 1994; Nielson, 2000), but while many studies have examined the relationship between germination and soil moisture content (Parker and Taylor, 1965; Wright et al., 1978; Bouaziz and Hicks, 1990; Blackshaw, 1991; Mian and Nafziger, 1994), most have used seed that was buried in the soil. Aerially seeded rye, however, is broadcast onto the surface of the soil and does not necessarily have good seed–soil contact. Surface soil moisture in the top few centimeters is highly variable and can change quickly compared with soil moisture deeper in the profile due to evaporation driven by direct interaction with the atmosphere (Hillel, 1998). Changes in soil moisture content are accompanied by changes in soil matric potential and hydraulic conductivity. Both are important for germination and emergence because the rate of water imbibition of ungerminated seeds is a function of the matric potential gradient between soil and seed (Hunter and Erickson, 1952; Evans and Etherington, 1990), mediated by the hydraulic conductivity of the soil.

The objectives of this study were to: (i) determine the physical and chemical properties that affect aerially seeded rye establishment in corn and soybean; (ii) characterize the amount of N removed from the soil by winter rye following corn and soybean; (iii) under laboratory conditions, determine the effect of varying temperature and surface soil moisture contents and water potentials on germination of rye on the soil surface; and (iv) develop a simple model to predict germination percentages based on soil moisture content.

**MATERIALS AND METHODS**

**Field Study**

This study was conducted during three fall seasons (2009–2011) at multiple locations in Dakota, Fillmore, Goodhue, Olmsted, Wabasha, and Winona counties in southeastern Minnesota (Fig. 1). This area has a typical interior continental climate with cold winters (−9°C mean temperature) and moderately hot
summers (20°C mean temperature). Sites were located on private farms and managed by the individual farmer-cooperators. Uncertified Rymin rye was aerially seeded via helicopter at approximately 112 kg ha\(^{-1}\) into standing silage or grain corn in 2009 and 2010 (22 sites) and into standing soybean in 2010 and 2011 (nine sites) (Table 1). Field sizes ranged from 2 to 20 ha. On the day of seeding, subsamples of seed were collected for wet-towel germination tests (Quarberg and Jahns, 2000), which showed rye germination to exceed 90% each year.

To determine which factors affect rye germination and establishment, we measured a variety of soil and weather characteristics. On the day of seeding, a sample area was selected in each of the 31 fields at least 15 m from the field edge or head rows and mapped with a GPS unit. Nine subsamples for soil characteristics were taken from a 3 by 3 grid, with each subsample being approximately 7.5 m apart. Soil moisture in the top 4 cm was determined with a TH2O soil moisture meter (Dynamax) and values were averaged. Next, soil samples were collected from 0 to 15 cm and combined at each site for a range of soil tests. Soils were air dried and ground to pass through a 2-mm sieve. Tests included organic matter (by loss-on-ignition), pH, Bray P or Olsen P (depending on pH), and K (Brown, 1998). Total N and C were measured via combustion analysis (Variomax CN Analyzer, Elementar Analysensysteme GmbH), and 2 mol L\(^{-1}\) KCl extractable NO\(_3\)–N and NH\(_4\)–N were determined by the diffusion-conductivity method (Carlson et al., 1990). Approximately 5 to 7 d after seeding, sites were resampled for soil moisture, and the seeding rate was estimated by counting the seeds on the soil surface. As expected, however, multicollinearity was found among several of the predictor variables, including: soil moisture content and precipitation; P and K contents; and organic matter, total N, and total C contents. Potassium was dropped from the analysis because levels were correlated with soil P levels. Precipitation is easier for a farmer to measure than soil moisture, so the latter variable was dropped. We also chose to keep precipitation 7 DAS instead of 2 DBS because several anecdotal reports stated that rain is needed shortly after seeding to ensure germination (Minnesota Department of Agriculture, 2008, p. 31–35; Mutch and Martin, 2010; NRCS, 2010). Finally, because farmers are likely to know the organic matter content of their soils, total N and C were also dropped from the analysis. Thus, the set of predictor variables evaluated included harvest date of the main crop, seeding rate, soil surface residue, inorganic N, pH, P, organic matter, precipitation 7 DAS, and GDD. In addition to these analyses, the relationship between total N uptake and biomass yields was examined using PROC REG (SAS Institute, 2009). Interactions and main effects were considered significant at \(P \leq 0.05\).

### Germination Study

Rye seeds were germinated on various soil types and at different water potentials and temperatures at the University of Minnesota, Saint Paul. The experimental design was a 3 \(\times\) 3 \(\times\) 3 factorial randomized complete block design with four replicates. The three factors included soil type, water potential, and temperature. Three soil types were chosen to represent a range of water holding capacities and soil textures across the state: a sandy loam (coarse-loamy, mixed, superactive, mesic Mollic Hapludalf) from near Marion, MN (Olmsted County); a silt loam (fine-silty, mixed, superactive, mesic Mollic Hapludalf) from near Elgin, MN (Wabasha County); and a clay loam (fine-loamy, mixed, superactive, frigid Calcic Argiudoll)
from near Morris, MN (Stevens County). Soils were collected in bulk from the top 15 cm of the Ap horizon during October 2009, air dried, and ground to pass through a 2-mm sieve. The soils were tested for organic matter, pH, Bray P, NH₄OAc-extractable K, total N, and total C in the same manner as discussed for the field study.

For each soil type, the amount of air-dried soil needed to reach a bulk density of 1.0 g cm⁻³ or greater was weighed out and mixed with enough deionized water to make a slurry. The slurry was poured into empty soil sample rings on top of saturated ceramic plates and the water potential was adjusted to −50, −200, or −500 kPa with a high-range pressure plate system (Klute, 1986). Once equilibrated, the soils were removed from the pressure system, and subsamples were taken to determine the gravimetric soil moisture content.

Experimental units were soils packed into individual, labeled petri dishes (100-mm diameter by 10 mm high) so that the soil depth was 0.7 cm. This was equivalent to approximately 29 g of oven-dried soil. Uncertified Rymin rye seed, which is widely used by farmers in the region, was used in this study. A wet-towel germination test (Quarberg and Jahns, 2000) with a minimum of four replicates verified the 80% germination rate stated on the label by the supplier. Thirty seeds were randomly placed on the soil surface in each petri dish. After lids were placed on each dish, the dishes were scaled in plastic bags to reduce moisture loss.

Three low-temperature incubators were set at 10, 18, and 25°C, respectively. These temperatures were chosen to represent below-average, average and above-average temperature scenarios in mid-September, when aerially seeding is likely to occur. Within each incubator, replicates were placed at the same approximate location, with Replicates 1 and 2 always placed above Replicates 3 and 4 in the center of the incubator.

Germination, or radicle emergence >2 mm (Bewely and Black, 2010–2011) were compared with 30-yr means (Table 2). The three counties listed in Table 2 contained most of the seeding sites. Precipitation was generally above average in 2009 and 2010 although the timing was different, with more rain earlier in the season of 2010, while 2011 was drier than normal. In all 3 yr, temperatures tended to be cooler than average.

In 2009, there was adequate precipitation before seeding in Fillmore County, but the more northern counties (Olmsted and Dakota) were considerably drier (Fig. 2). Precipitation in 2010 was ideal, as there was rain before and after seeding. In 2011, the northern counties were drier again, but Fillmore County received approximately 2 cm of rain after seeding.

Growing degree days from the time of seeding until biomass harvested averaged 549 in 2009, 539 in 2010, and 341 GDD in 2011. Due to a later seeding date, the lower number of GDD in 2011 may have limited establishment; however, we note that Aroostook rye, which, like Rymin, was developed for northern climates, can establish with 260 to 350 GDD (NRCS, 2002).

Soil characteristics: Mean soil moisture content, nutrient concentrations, pH, organic matter content, and surface residue cover are shown in Table 3. Soil moisture tended to decrease from the day of seeding to 5 to 7 DAS in 2009 and

\[ R^2 = \frac{CTSS - SSE}{CTSS} \]

where \( R^2 \) is the fraction of the variation in the dependent variable as explained by the model, CTSS is the correct total sums of squares, and SSE is the sums of squares of the error found in the PROC NLIM output (Robbins et al., 2006).

**RESULTS AND DISCUSSION**

**Field Study**

**Biomass Predictors**

**Weather:** Mean temperature and precipitation for each fall (2009–2011) were compared with 30-yr means (Table 2). The three counties listed in Table 2 contained most of the seeding sites. Precipitation was generally above average in 2009 and 2010 although the timing was different, with more rain earlier in the season of 2010, while 2011 was drier than normal. In all 3 yr, temperatures tended to be cooler than average.

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**Table 2. Average monthly weather conditions in southeastern Minnesota during the study years compared with the 30-yr mean (1971–2000, Minnesota Climatology Working Group, 2012).**

<table>
<thead>
<tr>
<th>Month</th>
<th>Precipitation</th>
<th>Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2009</td>
<td>2010</td>
</tr>
<tr>
<td>Dakota County</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept.</td>
<td>1.5</td>
<td>16.1</td>
</tr>
<tr>
<td>Oct.</td>
<td>15.5</td>
<td>4.7</td>
</tr>
<tr>
<td>Nov.</td>
<td>1.4</td>
<td>6.0</td>
</tr>
<tr>
<td>Dec.</td>
<td>5.8</td>
<td>6.2</td>
</tr>
<tr>
<td>Olmsted County</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept.</td>
<td>2.7</td>
<td>27.1</td>
</tr>
<tr>
<td>Oct.</td>
<td>16.4</td>
<td>1.6</td>
</tr>
<tr>
<td>Nov.</td>
<td>1.3</td>
<td>6.9</td>
</tr>
<tr>
<td>Dec.</td>
<td>5.6</td>
<td>4.1</td>
</tr>
<tr>
<td>Fillmore County</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept.</td>
<td>4.1</td>
<td>23.1</td>
</tr>
<tr>
<td>Oct.</td>
<td>17.2</td>
<td>2.6</td>
</tr>
<tr>
<td>Nov.</td>
<td>1.1</td>
<td>6.7</td>
</tr>
<tr>
<td>Dec.</td>
<td>6.9</td>
<td>8.4</td>
</tr>
</tbody>
</table>
2010, while it increased in 2011. Soil moisture content was highest in 2010 due to recent rainfall, while conditions were drier in 2009 and 2011. Residual soil inorganic N in the top 15 cm was generally higher and more variable under corn than soybean, probably a result of variability in fertilizer N applied at each corn site. Average P levels were considered very high (>21 mg kg\(^{-1}\)) at most sites, while K levels ranged from low (41–80 mg kg\(^{-1}\)) to very high (>160 mg kg\(^{-1}\)) (Rehm et al., 2006). Organic matter content and pH were relatively stable across years and sites, as were total N and C. Surface residue cover in corn averaged around 25% in both 2009 and 2010, although the standard deviation was high, probably due to the variety of tillage types used by the farmers in this study.

Management practices: Actual rye seeding rates varied from the estimated seeding rate of 112 kg ha\(^{-1}\). In corn, the actual seeding rate was 37.3 ± 6.1 and 22.6 ± 6.2 kg ha\(^{-1}\) in 2009 and 2010, respectively. For soybean, the seeding rate was 64.6 ± 22.5 kg ha\(^{-1}\) in 2011. We observed seeds caught in the corn canopy in several fields, which may explain some of the differences seen in the corn and soybean crops. Additionally, these counts were taken 5 to 7 DAS and there may have been some unexplained losses of seed in that time period.

The harvest date of the main crop was 34.0 ± 0.4 and 28.4 ± 2.4 DAS for soybean in 2010 and 2011, respectively, and 72.1 ± 5.3 and 36.0 ± 13.9 DAS for corn in 2009 and 2010, respectively. Corn was harvested for grain as well as silage in this study, which explains the high standard error.

Biomass Production

Biomass: Aboveground rye biomass averaged 26.4 kg ha\(^{-1}\) in corn in 2009, 505.9 kg ha\(^{-1}\) in corn in 2010, 270.6 kg ha\(^{-1}\) in soybean in 2010, and 66.3 kg ha\(^{-1}\) in soybean in 2011 (Fig. 3). Altogether, however, most sites (60%) had <50 kg ha\(^{-1}\). Biomass tended to be lower in 2009 and 2011 compared with fall rye biomass reported in Ontario, Canada, where rye biomass ranged from 91 to 884 kg ha\(^{-1}\) after being broadcast into standing corn in August (Ball-Coelho and Roy, 1997). In Iowa, the average biomass for rye overseeded into soybean was...
410 kg ha\(^{-1}\) (Johnson et al., 1998). Both of these locations have longer growing seasons (an average of 160 d vs. 140 d in southeastern Minnesota), which may explain some of the differences. In 2010, however, the wettest year of the study, biomass yields were similar to those reported in Ontario and Iowa despite cooler than average temperatures.

**Biomass prediction:** For three of the variables under consideration (harvest date, seeding rate, and residue cover) data were available for only 13 of the 31 sites; however, an initial multiple regression for those 13 sites revealed that none of the three variables was significant, so they were subsequently dropped from consideration.

The second analysis included all 31 sites and the following variables: inorganic N, pH, P, organic matter, precipitation 7 DAS, and GDD. The best model, as selected by the lowest Akaike information criterion (AIC) value, suggested a significant relationship between fall biomass and total precipitation 7 DAS (\(R^2 = 0.43; F = 22.94; P < 0.001\)):

\[
\text{Biomass} = 78.1(\text{Precipitation 7 DAS})
\]

where Biomass is fall aboveground rye dry matter (kg ha\(^{-1}\)) and Precipitation 7 DAS is the total cumulative amount of precipitation (cm) for the 7 d following seeding. Adding additional variables did not significantly increase \(R^2\) values.

Several reports have reached similar conclusions about the need for precipitation events close to the seeding date (Clark, 2007; Minnesota Department of Agriculture, 2008, p. 31–35; Mutch and Martin, 2010). The NRCS in Iowa suggested that precipitation is needed within 10 d if soil moisture on the day of seeding is not sufficient for germination (NRCS, 2010). Fisher et al. (2011) found that rye seedling emergence was more rapid when broadcast closer to rainfall events. One consideration is that precipitation 7 DAS was highly correlated with soil moisture content on the day of and 1 wk after seeding, indicating that the latter variables also may be important predictors of fall biomass production.

Our model accounted for only approximately 43\% of the variation in biomass production, however, despite having taken into account multiple possible variables. This indicates that there are additional factors that affect germination and establishment. For instance, Ball-Coelho and Roy (1997) suggest that light interception played an important role in increased rye biomass because the previous low-yielding corn crop in their study provided less light competition than in other years. Baker and Griffis (2009) also reported that rye biomass was reduced in their model if seeded too early into corn due to the low irradiance environment beneath the corn canopy. Several other successful models of rye growth take into consideration solar radiation interception, as well (Feyereisen et al., 2006; Whitmore and Shroder, 2007). In addition to light interception, canopy cover also influences soil temperature at the soil surface (Starks, 1996), which may have an effect on seed germination and survival.

Another possible factor is seed predation by insects and animals. Davis and Liebman (2003) found that predation of giant foxtail (Setaria faberi R.A.W. Herrm.), a weed often found in corn and soybean, peaked in September, with 5 to 18\% of seeds being eaten per day. Most of our seeding happened in September and we noticed unexplained losses of seed at some sites, so it is likely that predation occurred. In fact, a motion-sensitive camera recorded rodents eating the seed in one soybean field (Supplementary Fig. S1). Barnett and Comeau (1980) reported that much of the exposed seed in their study was eaten by birds. At several of our sites, we also noticed that the emerging coleoptiles of germinating rye seed were eaten. Similarly, in another study, ground beetles damaged the endosperm of germinating perennial ryegrass (Luff, 1980). Further research to help determine the mechanism by which most seed is lost may be helpful in improving management practices for aerial seeding.

**Nitrogen uptake:** The average N concentration of the rye was 37.9 ± 6.6 g kg\(^{-1}\) across all sites and previous crops. Fall total N uptake values ranged from 0.1 to 44.7 kg ha\(^{-1}\), similar to those reported by Ball-Coelho and Roy (1997), which were 2.6 to 40.7 kg ha\(^{-1}\). They concluded that rye was a good N scavenger because N uptake increased with increasing N fertilizer rates for the previous corn crop. This is an important characteristic of a rye cover crop, as previous studies have reported substantial N losses in corn and soybean systems. For instance, in row crops, tile drainage losses ranged from 14 to 105 kg N ha\(^{-1}\) yr\(^{-1}\) (Kladivko et al., 1999; Strock et al., 2004), while losses measured by lysimeter were 9 to 118 kg N ha\(^{-1}\) yr\(^{-1}\) (Zhu and Fox, 2003).

Not surprisingly, a strong relationship (\(F = 6159.5, P < 0.001\)) was found between biomass production and total N uptake (Fig. 4), despite the fact that the inorganic N content of the soil was not a factor in biomass production. We found that approximately 300 kg biomass ha\(^{-1}\) was needed to take up 10 kg N ha\(^{-1}\). Only 16\% of our 31 sites produced biomass >300 kg ha\(^{-1}\) during the fall. In Ontario, broadcast rye biomass also failed to accumulate this much dry matter in 2 out of 3 yr (Ball-Coelho and Roy, 1997). In Iowa, however, overseeded rye biomass averaged 410 kg ha\(^{-1}\) during three fall seasons (Johnson et al., 1998), probably due to more favorable weather and warmer soils. These results suggest that overseeding a rye cover crop, including aerial seeding, may not be of practical value in more northern climates if the sole intention is to scavenge N.
Germination Study

Total Germination

The soil × moisture interaction was significant for total germination ($P < 0.05$). At each water potential, the clay loam had the highest moisture content and the sandy loam had the lowest (Fig. 5). Across the range considered in this study, water potential did not affect germination for the clay or silt loam, but it did have an effect in the sandy loam, where germination was reduced at $-500 \text{kPa}$ (Fig. 6). Water potential accounted for only 13% of the variability in the germination data ($P = 0.071$) (data not shown), while moisture content accounted for 46% of the variability ($P < 0.001$) (Fig. 7). These findings are contrary to the well-documented theory that germination is controlled by water potential (Hunter and Erickson, 1952; Hadas and Russo, 1974; Benech-Arnold and Sanchez, 2004). Most of those studies, however, used seed that was buried in the soil, with good seed–soil (and hence soil water–seed) contact.

On the other hand, one study that germinated seeds on the surface of slate dust determined that in drier substrates moisture content appeared to be the limiting factor rather than water potential (Harper and Benton, 1966). Dasberg and Mendel (1971) found that the rate of water supply to the seed was a function of contact between the seed and soil, while Hadas and Russo (1974) reported that seeds in coarse-textured soils have smaller relative wetted areas. These factors may help to explain our results. With the limited amount of soil contact that the surface-applied seed had in the current study, it was more likely to be in contact with water in the clay than in the sand at any given water potential. Collis-George and Sands (1959) and Dasberg and Mendel (1971) argued that hydraulic conductivity may also play a large role in controlling the germination rate because drier soils have less ability to transmit water to the seed. This would be especially true of sandy soils, which transmit water more slowly than clay soils under unsaturated conditions (Bouma and Denning, 1972). In contrast, Wuest et al. (1999) concluded that seed–soil contact is not necessary for germination and that water transport to imbibing seeds takes place primarily in the vapor phase. The slower germination that we observed in the sandy
loam at –500 kPa relative to the finer textured soils supports the notion that liquid flow is the more dominant mechanism.

**Total Germination Model**

The quadratic plateau model used to describe the relationship between germination and moisture content discussed above (Fig. 7) was also used to predict the moisture needed for optimal germination. The critical moisture content was 0.083 g g⁻¹, above which germination was not affected by moisture content. Below this threshold, germination was drastically reduced, following a quadratic decline down to 0.051 g g⁻¹, below which germination did not occur:

\[
G = -496.8 + 14046.1W - 84823.2W^2
\]

where \(G\) is the total germination (%) and \(W\) is the gravimetric moisture content.

**Germination Timing**

The soil type × water potential interaction was significant \((P < 0.05)\) for TG₅₀ (Fig. 8). At –50 kPa, TG₅₀ was approximately 2 d in all soils. This was maintained at all moisture levels in the clay loam. A delay of 1.3 d in germination was found in the silt loam between –50 and –500 kPa tension, although these differences were not significant \((P = 0.12)\). In the sandy loam, decreasing water potential delayed germination by 1.9 and 6 d at –200 and –500 kPa, respectively. The differences across soil types at similar water potentials further demonstrates that moisture content and hydraulic conductivity may play a larger role in germination than water potentials, particularly when the seed has limited soil contact. When comparing fine sand to a “black earth” soil, Collis-George and Sands (1959) similarly found that the rate of seedling germination was reduced as soil tension increased.

Temperature also significantly affected TG₆₀ \((P < 0.05)\), with values of 4.6, 2.8, and 3.1 d at 10, 18, and 25°C, respectively. Germination was delayed by 1.8 d when the temperature decreased from 18 to 10°C. A slight delay (0.3 d) was seen between 18 and 25°C, but the difference was not significant \((P = 0.60)\). Wright et al. (1978) found that increasing the temperature from 21 to 28°C generally decreased seedling emergence in a clay soil, particularly at drier water potentials.

Some studies have documented that the emergence rate of seedlings was more influenced by temperature than soil moisture (Cutforth et al., 1985; Blackshaw, 1991). In the current study, the opposite appeared to be true in the sandy loam, although the range of temperatures was not as large as in previous studies. Furthermore, Cutforth et al. (1985) found that the soil moisture content influenced the germination rate at high temperatures (30.5°C) but not at low temperatures (15°C). We did not find this to be the case because temperature effects were independent of the soil type × water potential interaction.

**CONCLUSIONS**

Under the conditions of this research, we found that precipitation within a week of aerial seeding is the most important factor in determining successful establishment of rye. Because precipitation and soil moisture content were highly correlated, however, the latter variable may be important as well. In practice, producers may want to consider alternative planting methods to aerial seeding if soil conditions are dry and precipitation is not forecast within a week. Additional factors such as light interception through the canopy and seed predators were not considered in the analysis and may also play a role in establishment. A priority for research should be the characterization of cover crop seed predators and the testing of strategies to reduce seed losses.

The amount of N scavenged by the rye varied and was related to biomass production. We found that at least 300 kg ha⁻¹ of rye was needed to take up 10 kg N ha⁻¹, but only 16% of our sites produced this amount of biomass before the ground froze during the period of this research. Aerial seeding was not compared with other planting methods in the current study, so it is unclear if N uptake would be impacted by placement of the seed on top of or buried in the soil. It is likely that areas with a longer growing season may experience more benefit from the use of cover crops if the main goal is to scavenge N.

Germination of rye on the soil surface under laboratory conditions was found to be more strongly dependent on moisture content than water potential. A quadratic plateau model suggested that germination will decline rapidly below a moisture content of 0.083 g g⁻¹ and will cease below 0.051 g g⁻¹. Germination timing was delayed only in the sandy loam at the lowest water potential, further indicating that hydraulic conductivity plays a role in the germination of seeds on the soil surface. These findings suggest that overseeding onto coarse-textured soils should be avoided if there has not been a recent rainfall or if rainfall is not expected within the days following seeding.

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