

THESIS

EVALUATION OF SPRING WHEAT GENOTYPIC RESPONSE
TO SOIL HEALTH PROMOTING MANAGEMENT PRACTICES

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ABSTRACT

EVALUATION OF SPRING WHEAT GENOTYPIC RESPONSE TO SOIL HEALTH PROMOTING MANAGEMENT PRACTICES

Growing efforts to restore soil organic matter and overall soil health are likely to enhance soil biological communities and promote positive interactions between plants and soil communities. However, modern genotypes bred under intensive management practices may not be able to benefit fully from soil health promoting practices if they have lost their ability to effectively interact with key soil organisms. The purpose of this study was to explore this idea by studying how spring wheat genotypes with different breeding contexts and histories respond to improved soil health achieved via additions of organic matter and soil fauna.

A greenhouse experiment with a full factorial complete randomized design was carried out at Colorado State University, Fort Collins, between June and November, 2016. The treatment factors included spring wheat genotype, as well as compost and earthworm additions. The genotypes included a wild ancestor of wheat, *Aegilops tauschii*, two older genotypes of spring wheat, Gypsum and Red Fife, and two near-isogenic modern genotypes, Scholar Rht2M and Scholar Rht2W, that differ only by the presence of the semi-dwarf allele *Rht-D1b* in ScholarRht2M. Each wheat genotype was grown in rootboxes (24.5 x 3.5 x 38.0 cm) that received either soils amended with composted manure or not, and with or without the addition of earthworms (two *Aporrectodea caliginosa* per box). Measurements included plant growth (heading date, number of tillers), biomass (aboveground and root biomass, root:shoot ratio), root morphology (root length and diameter), yield-related traits (number of seeds, seeds weight,

average weight per seed, harvest index), nitrogen content (vegetative aboveground and grains), and nitrogen uptake.

Findings indicate that interactions between genotypes and soil treatments were inconsistent, and the original hypothesis, that older wheat genotypes would show a greater response to improved soil biological conditions relative to newer genotypes, was not well supported. Overall, the aboveground and yield responses to compost were small compared to the root responses. Composted manure additions, increased root length, biomass, and diameter only in the wild accession (*Ae. tauschii*) and older Gypsum wheat variety. Modern genotypes, on the other hand, exhibited little root trait plasticity except in root diameter, which decreased with compost additions. Except for a decrease observed in Red Fife, compost effects on aboveground biomass were not significant for most genotypes. Genotype x earthworm interactions were only observed in the vegetative biomass N uptake, and earthworm effects in general were low due to low survival of the earthworms. *Ae. tauschii* and Gypsum had a more positive response to compost addition for both aboveground and root biomass, indicating that these genotypes may better take advantage of soil health promoting practices. While Gypsum had a similar response to the wild accession when compost was added, Red Fife tended to respond more like the modern genotypes.

Overall, my findings suggest that different wheat genotypes can respond distinctly to changes in soil management and biological activity. Only a few genotypes were tested, but a number of clear genotype x soil biology interactions highlights the importance of considering soil management practices, environmental context, and breeding history for different wheat lines, so that we can better manage plant x soil interactions.

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INTRODUCTION

Plant-soil feedbacks can benefit both plants and soil biological communities through such mechanisms as improved plant nutrient availability and belowground C inputs to support soil biological communities. These beneficial plant-soil feedbacks are now being examined as a potential approach for improving agricultural sustainability and soil health (Chaparro et al., 2012; Huang et al., 2014). The challenge in this, however, is that most of today's crops have been bred under intensive management practices that favor a reduced crop reliance on plant-soil interactions; for example, pest management and nutrient needs are largely met through external chemical applications. Though significant breeding work has focused on pest and disease resistance and nutrient use efficiency, there is a lack of crop genotypes specifically targeted for phenotypic traits that support plant-soil interactions that mediate key agroecosystem functions. Aggravating this disconnect, is that modern intensive agricultural practices (e.g. application of pesticides, inorganic fertilizers and tillage) often have harmful impacts on soil biological communities. Thus, even if crop traits that facilitate plant-soil feedbacks can be identified, the biological community may be inhibited by the agricultural practices in place. The increasing trend towards agricultural practices that improve soil health (e.g. no-till, cover crops, organic amendment additions), may require that we better identify crop traits in concert with managements practices that enhance beneficial plant-soil interactions. Here I examine how genotypes along a gradient of historical breeding have altered phenotypic traits such as root growth, and how differences in such traits impact genotype growth responses to soil health improvements.

Since the Green Revolution, agricultural systems in much of the world, have shifted to include large scale monocropping, intensive tillage, high inputs of synthetic fertilizer, and increasing pesticide application (Lichtfouse et al., 2009). The onset of modern intensive agriculture coincides with breeding efforts focused on producing genotypes with high yield and harvest index that are more responsive to highly labile nutrient inputs, such as inorganic fertilizer. These genotypes sometimes, but not always, support lower belowground biomass (Van Bueren et al., 2011; Awad, 2015). More recently, organic agriculture and other soil health promoting practices that typically rely more on biologically-mediated nutrient availability are on the rise globally. This is in part due to widespread concern over the detrimental impacts of intensive, high-input agriculture on soil health and climate change (Mulvaney et al., 2009; Van Eerd et al., 2014). Indeed, significant growth rates of organic agriculture have occurred for much of the 21st century. Compared with 1999, when 11 million ha were under organic agricultural management globally, in 2014 the area quadrupled (43.7 million ha) (Willer and Lernoud, 2016), while other practices such as cover-cropping and no-till farming have also gained in popularity. Despite this growing trend, most crop genotypes used in organic production systems or systems with greater reliance on plant-soil interactions have been selected under conventional practices (Van Bueren et al., 2011). Crop genotypes selected in such environments may be less able to take advantage of (and support) soil biological activities and a range of mutualistic interactions between plants and soil organisms.

Much effort to improve soil health focuses on restoring soil organic matter (SOM) and associated biological communities that promote positive interactions between plants and soil communities (Adesemoye and Kloepper, 2009; Dinnes et al., 2002; Thangarajan et al., 2013). Soil organisms regulate many soil functions including organic matter decomposition, nutrient

transformations, maintenance and formation of soil structure, and biocontrol of soil-borne plant pathogens and pests (Powelson et al., 2011). While plants benefit from diverse, active soil organisms, they in turn, contribute to belowground soil communities via carbon (C) inputs (e.g., roots, aboveground biomass, and root exudates) that form the primary substrate for belowground food webs (Grayston et al., 1998; Marschner et al., 2001; Bais et al., 2006). These interactions between crops and soil biota can be easily disrupted or promoted, as soil microbes and fauna are highly sensitive to changes in soil management such as tillage (Piovanelli et al., 2006), fertilization (Wu et al., 2011) or organic amendments (Kallenbach and Grandy, 2011). Among other strategies, the addition of compost or manure has been shown to stimulate soil biological activities, including earthworm populations (Binet et al., 1998; Chaudhry et al., 2012), and can improve a range of soil physical (Celik et al., 2004; Fonte et al., 2012) and chemical properties (Schlegel, 1992; Araujo et al., 2004) as well as root growth (Baldi et al., 2010; Baldi and Toselli, 2013). However, modern crop genotypes may not fully be able to benefit from soil health promoting practices if they have lost their ability to effectively interact with key soil organisms.

Optimizing the benefit of specific agricultural practices that improve soil health could include the use of adapted genotypes exhibiting traits that best take advantage of improved soil conditions and associated benefits to soil biological function (Noguera et al., 2011; Bakker et al., 2012). Genotype traits, however, can be plastic, exhibiting variability in response to specific agricultural practices. For example, studies by Murphy et al. (2007) and Wortman et al. (2013) showed that the highest yielding wheat genotypes in conventional systems are not always the highest in organic systems, indicating that genotypic adaptability is partially responsible for the yields. Plasticity of different genotypes in response to belowground activities is also likely to occur and thus may be key to amplifying the benefits of soil health promoting practices. A

comparison of old and modern crop genotypes could serve as a useful framework for examining this based on co-occurring historical changes in breeding environments and trait selections.

Historical genotypic gradients have previously been shown to respond differently to environmental modifications such as drought (Fan et al., 2009; Young'an et al., 2010) and CO₂ enrichment (Manderscheid and Weigel, 1997; Franzaring et al., 2014). I propose that crop wild ancestors may have trait advantages to utilize soil biological activities as they occur in natural environments, relying heavily on plant-soil feedbacks. The greater usage of organic inputs instead of synthetic fertilizer before the Green Revolution may have also preserved the ability of older genotypes to interact with belowground communities. Thus, old genotypes typically cultivated with limited external inputs, would be expected to have greater positive response to soil health promoting practices relative to modern genotypes. Moreover, the transition from wild ecosystems to modern agriculture may have altered morphology and ecophysiology (Schmidt et al., 2016), impacting how crops acquire nutrients and allocate C belowground. In addition to a higher root:shoot ratio which may favor a more active and diverse soil biological community, certain plant traits such as root diameter and specific root length are key in determining nutrient uptake and efficiency (Sattelmacher et al., 1994). Recently, root traits have been used to identify plant nutrient acquisition strategies (Kong et al., 2014; Paez-Garcia et al., 2015). In uncultivated natural environments, wild plants exhibit a tradeoff between rapid growth (often associated with small root diameter) and nutrient conservation, which can translate to higher nutrient use efficiency. It remains unclear if this tradeoff exists in crops, but if it does, modern, high-yielding genotypes with relatively faster growth rates may exhibit root traits that result in different nutrient economies. Wheat, representing about 20% of human food supply (CGIAR, 2014), is

one of the first domesticated crops, with a long history of breeding and thus is a relevant crop species for a genotype historical gradient framework.

Bread wheat (*Triticum aestivum*) probably originated only after the domestication of diploid and tetraploid wheats (Feldman, 2001). The early forms of wheat were diploid (genome AA) (einkorn, *Triticum monococcum*) and tetraploid (genome AABB) (emmer, *Triticum dicoccon*) (Shewry, 2009). Tetraploid wheat later crossed to diploid goat grass (*Aegilops tauschii*) resulting in hexaploid wheats (genome AABBDD), including bread wheats (*Triticum aestivum*) (Daud and Gustafson, 1996). Therefore, *Aegilops tauschii* was the donor of the D genome of hexaploid wheats. Wheat was first cultivated in wild and domesticated form (10,300-7,500 BP), marking the beginning of wheat breeding activities. Since then, modern wheat genotypes have been developed through three main phases: occasional and sometimes non-intentional selection by the earliest farmers, more deliberate selection in polymorphic fields, and selection in monomorphic fields as part of more modern breeding approaches (Feldman, 2001). In the early stages of cultivation, farmers used landraces specific to the local agroecosystem conditions. As demand increased, selection activities were encouraged to obtain genotypes with high yield potential, tolerant to diseases, and adapted to harsh environments. In the late 1960s, the breeding of high-yielding genotypes was fundamental in supporting the Green Revolution, along with wide-spread use of chemical fertilizers, pesticides, controlled water supply, and mechanization. In this period, the semi-dwarf (*Rht*) genes were also introduced, and today most modern wheat genotypes contain one or more of these genes. As wheat breeding advanced, modern genotypes may have become increasingly different from their ancestors physiologically and phenotypically as well as in their ability to benefit from soil biological activities (Pérez-Jaramillo et al., 2016).

In this study, I sought to understand how wheat genotypes respond to improved soil health, achieved via additions of organic matter and key soil fauna. This study explored how representative genotypes, from wild-accession ancestors, to pre-Green Revolution genotypes, to ‘modern’ genotypes, respond to compost and earthworm treatments (here considered components or proxies of soil health). I hypothesized that older genotypes (wild accession and old genotypes) would respond more (in growth and yield) to compost and earthworm additions than modern genotypes.

MATERIALS AND METHODS

Experimental Design and Implementation

This study was carried out in a greenhouse at Colorado State University, Fort Collins, between June and November, 2016. The study was arranged based on full factorial complete randomized design (CRD) with three factors: genotype (5 levels), compost (2 levels), and earthworm (2 levels). Different genotypes of spring wheat (*Triticum aestivum*) were grown to understand the interactive impacts of phenotypic trait variations, earthworms and compost on a genotype of wheat growth parameters. The genotypes included one accession of Tausch's goatgrass (*Aegilops tauschii*), considered a wild ancestor of wheat (Accession number: TA2374) and accessed from Pakistan in 1955 (genesys-pgr.org, 2017). The *Ae. tauschii* seeds were from the Wheat Genetics Resource Center, Manhattan, Kansas. Two older genotypes of spring wheat were 'Gypsum' and 'Red Fife'. Gypsum was bred in Colorado, USA (Clark et al., 1922) and was released in 1912, while Red Fife was developed as early as 1842, originating from Ukraine (Symko, 2002) though another study suggested it originated in Poland (Morris et al., 2001). The Gypsum and Red Fife seeds were from the USDA-ARS National Small Grains Collection, Aberdeen, Idaho. The two modern genotypes, Scholar Rht2M and Scholar Rht2W, originated in Montana, USA. Scholar Rht2W was released as the cultivar 'Scholar' (PI607557) in 2000 (Lanning et al., 2000), while experimental line Scholar Rht2M was described in 2012 (Lanning et al., 2012). The modern genotypes are near-isogenic to each other; Scholar Rht2W contains the tall allele *Rht-D1a* at the *Rht-D1* locus, while Scholar Rht2M contains the semi-dwarf allele *Rht-D1b*. The Scholar near-isogenic lines were obtained from Luther Talbert, Montana State University, Bozeman, Montana.

The compost treatments included either soils amended with composted manure (from the Aurora Dairy in Greeley, Colorado) or soils without compost. Fresh manure compost was passed through a 4.0 mm sieve prior to application at a rate of 300 ml per box. For the earthworm treatment, each box either received two earthworms per box or no earthworm addition. The earthworms used in this study, *Aporrectodea caliginosa*, are commonly found in Colorado (Reynolds, 2011; McDaniel, 2012) and were collected from ARDEC within the top 30 cm of soil from a nearby field to where soil was collected. Upon collection, earthworms were rinsed with water and patted dry for weighing. Only earthworms weighing between 0.75 and 1.00 g were used to ensure uniformity of this treatment.

Topsoil (0-20 cm depth), used as a growth media in the experiment, was collected from the Agricultural Research, Development and Education Center (ARDEC) located 6.5 km north of Fort Collins, Colorado (40°39'10.3"N 104°59'46.6"W). The soil is a clay loam, mixed, superactive, mesic Aridic Haplustalfs soil (Liu et al., 2005) and contains 2.2% organic matter, pH 9.0, 17.7 ppm N, 86.5 ppm P, and 314.5 ppm K. The soil was first sieved (4.0 mm), air-dried for 48 hours, and then mixed with sand (1:1 volume) to avoid soil compaction and maintain drainage. Plants were grown in 24.5 cm x 3.5 cm x 38.0 cm deep rectangular plastic box, hereafter called rootboxes (Fort Collins Plastics, Fort Collins, CO USA) (Schultz, 2008). Each box was filled with the sand-soil media to 4700 g box⁻¹, and packed by gentle shaking. The rootboxes were angled 25° and had one side that could be opened for root observations and rhizosphere sampling in a complementary study (Kallenbach et al. in prep). Each box was covered with white shade cloth to reduce light infiltration. The rootboxes were placed on a bench in the middle of the greenhouse and thus the temperature and humidity were assumed to be uniform for all the plants.

I mixed in 1.0 g of NPK 16-16-16 fertilizer to 5-6 cm depth in each box prior to seeding for basic nutrients for early growth of the plants. That dose was considered as low rate to avoid confounding effect of desired fertilizer to compost and earthworm effects. Direct seeding (two seeds per box) was applied for old and modern genotypes on June 9, 2016. Two seeds per box were planted at 2-3 cm depth. For *Ae. tauschii*, a cold treatment was used to enhance germination rate. I rolled the *Ae. tauschii* seeds in wet tissue paper and kept inside a drawer for 3 days, moved to cold storage at 4^o C for 4 days, then placed them back into the drawer for another 3 days. After that, two seedlings (~ 3 cm height) were transplanted per box. Thinning to one plant per box was carried out two weeks after planting for all treatments. Five replications were established for each treatment leading to 100 plants in total.

All plants were grown in greenhouse under natural light, but supplemented with 600 watt lamps as needed to achieve a 16 hr growing day, and was provided with air circulation and misting system to maintain temperature and humidity. All plants were established at 26^o C and 40% humidity until 18 days after planting at which point plants were grown at 21^o C and 50% humidity until harvest. Soils were maintained at approximately 70% soil water holding capacity until wheat plants reached the mealy ripe stage (Feekes code 11.2), after which soil moisture was lowered to 60% until harvest. Pests, mainly aphids, were controlled as needed using light insecticide application.

Plant Growth and Yield Assessment

Heading date and number of tillers were recorded for each plant in the study. Following harvest, I measured aboveground and root biomass, seed weight per plant, root morphology characteristics, and N content of the grain and vegetative aboveground biomass (details provided

below). Heading date was recorded when the spike emerged fully above the flag leaf (Lollato, 2016). Number of tillers was counted one day before harvest. Physiological maturity was determined when the peduncle of the first head had turned completely yellow. Harvest was carried out separately for each genotype when 50% of the plants in treatments of the same genotype reached physiological maturity. Total aboveground biomass was harvested by cutting stems just above the soil surface and drying at 60^o C. Total biomass is reported as the sum of aboveground biomass and root biomass. Number of seeds was counted after threshing the spikelets manually and then yield was determined as the total weight of seeds per plant. The average weight per seed was calculated by dividing yield by the number of seeds per plant. Harvest index was determined as the total weight of seeds per plant divided by total aboveground biomass.

Following aboveground biomass collection, the soil was examined for the presence of earthworms and rinsed with tap water to separate coarse roots from the soil. The fine roots were separated from soil using an elutriator (Standard Industries Inc., Fargo, ND USA). Root morphology characteristics were determined using a root scanning procedure following Becker et al. (2016) on a ScanMaker 9800XL (Microtek International Inc., Santa Fe Spring, CA USA) with gray scale scanning type and 600 dpi resolution. To improve image contrast and root length estimates, all roots were submerged in staining liquid (Organic Neutral Red Stain) before scanning (Costa et al., 2001). I analyzed the scanned images with WinRhizo Regular software (Regent Instrument Inc., Quebec, Canada). The root diameter classes were set as 0.00 – 0.25, 0.25 – 0.50, 0.50 – 0.75, 0.75 - 1.00, and > 1.00 mm. Root morphology was evaluated using WinRhizo software and included root length, root surface area, root volume, average root diameter, and root length, surface area, and volume for each diameter class. After scanning, all

roots were washed using tap water and oven-dried at 60⁰ C for 72 hours and then weighed for total belowground biomass. Grain and aboveground biomass components (including stems, leaves, and chaff) were ground and analyzed separately for total N concentration using a TruSpec® CN (LECO Corporation, Saint Joseph, MI USA). Nitrogen uptake was calculated by multiplying N concentration by dry biomass.

Statistical Analysis

Data analysis was performed using R Statistical Software version 3.2.5 (R Development Core Team) in R Studio (version 1.0.136) environment. To satisfy ANOVA assumptions, variables were square root transformed as needed (heading date, above-ground biomass, root length, average root diameter, harvest index, and vegetative biomass N concentration) or log transformed (total aboveground N uptake). Three-way ANOVA with a CRD model was run for all factors as well as two- and three-way interactions. Least square means were estimated using lsmeans function and compared using Tukey method with $\alpha = 0.05$. Summary statistics are given in original units.

RESULTS

Maintenance of Treatments

Survival of plants was high, with only three plants dying over the course of the experiment. Additionally, two more were severely stunted, thus 95 plants (experimental units) were considered for analyses. Mortality and stunting did not appear to be influenced by the treatment in place. The earthworm manipulation was less successful, as most of the earthworms did not survive until the end of the experiment. However, evidence of their activities was observed throughout the first month (via surface casting) and at harvest, and significant burrowing and casting activity was noted in nearly all earthworm addition treatments, thus the earthworm factor was included in all analyses.

Plant Growth and Biomass

Genotype had significant impacts ($p < 0.001$) on all plant growth (heading date and number of tillers) and biomass variables (aboveground biomass, root biomass, total biomass, and root:shoot ratio; Table 1). Many of the differences were due to *Ae. tauschii*, which took nearly twice as long to reach heading, had more tillers, greater root biomass, and higher root:shoot ratio than the four *Triticum* genotypes. However, in the absence of *Ae. tauschii*, significant effects of genotypes were still observed for all of these variables, such that Gypsum generally had a longer time to reach heading (Table 1, Fig. 1A), had more tillers, higher above- and belowground biomass, and higher root:shoot ratio than the modern genotypes. Compost also had a significant main effect (across all genotypes) on the heading date and number of tillers ($p < 0.001$) as well

as root biomass ($p = 0.015$). Earthworms significantly delayed heading date by 2.7% on average ($p = 0.044$), but did not influence any of the other plant growth or biomass variables.

Significant interactions between genotype and compost for all growth and biomass variables suggest that the effect of compost depends on the genotype in question. For example, in *Ae. tauschii* the compost treatment nearly doubled the number of tillers and increased above- and belowground biomass by 60% and 158%, respectively (Table 1, Fig. 1B, 1D). While comparison of means did not suggest any effect of compost on the Gypsum, Rht2M, and Rht2W genotypes, the aboveground and total biomass of Red Fife were reduced by 30 and 35%, respectively, in the treatments with compost (Fig. 1C, 1E). No other significant interactions were observed for the plant growth and biomass variables.

Root Morphology

Root image analysis indicated that genotype also had significant effects on root length and average root diameter ($p < 0.001$; Table 2). *Ae. tauschii* demonstrated the greatest root length per pot (476 m), approximately three to five times that observed in the *Triticum* genotypes. Among wheat genotypes, Gypsum had the greatest root length (157 m), while Red Fife, Rht2M, and Rht2W showed similar root values of 88 m, 87 m, and 87 m, respectively. The average root diameter of *Ae. tauschii* was 1.04 mm, twice that of all wheat genotypes. Compost had a significant effect on root length ($p = 0.020$), but not for average root diameter. Overall, plants with compost addition had a 59% greater root length than plants without compost. Earthworms also showed a strong effect on root diameter. The root diameter average with earthworms' present was 0.72 mm, significantly lower than without earthworms (0.80 mm; $p < 0.001$).

A significant interaction between genotype and compost was observed for root length ($p = 0.002$) and average root diameter ($p < 0.001$; Table 2). The root length of *Ae. tauschii* more than doubled in the presence of compost, while Gypsum, Rht2M and Rht2W showed an increase of 46%, 22%, and 8%, respectively. Meanwhile, Red Fife showed a root length decrease (non-significant) of 21% in the presence of compost (Fig. 2A). Compost effects on root diameter also depended on the genotype. Average root diameters increased by 47% for *Ae. tauschii* in the presence of compost. Conversely, compost resulted in a significant decrease in root diameter for the modern genotypes, 20% in Rht2M and 25% in Rht2W, and had no significant effect on the old genotypes (Fig. 2B). The interaction of compost x earthworms also influenced root diameter ($p = 0.004$). In general, the treatments receiving compost and earthworms (C-E) exhibited the lowest root diameter (0.52 mm). No other significant interactions were observed for root length or average diameter (Table 2).

In examining root length distribution by diameter, roots were dominated by < 0.25 mm diameter roots (87.7%; Fig. 3). The rest consisted of 0.25 – 0.50 mm (10.0%), 0.5 – 0.75 mm (1.8%), 0.75 – 1.00 mm (0.4%), and > 1.00 mm (0.1%).

Yield

The modern genotypes Rht2M and Rht2W were the first to reach maturity followed by Gypsum (old genotype) 10 days later. Red Fife and the wild genotype were harvested one and two months, respectively, behind the modern genotypes. Genotype had significant effects on yield variables. *Ae. tauschii* accession had a higher number of seeds, but lower yield (total seed biomass), average seed weight, and harvest index compared to old and modern genotypes. Among the wheat genotypes, modern genotypes were highest in all yield variables except the

average seed weight (Table 3). For example, the modern genotypes demonstrated higher seed weight per plant (3.28 g plant⁻¹ for Rht2M and 2.79 g plant⁻¹ for Rht2W) than old genotypes (2.57 g plant⁻¹ for Gypsum and 2.56 g plant⁻¹ for Red Fife). The modern genotype Rht2M had the highest harvest index (0.33) among wheat genotypes, which was not significantly different from Rht2W (0.28) and Red Fife (0.28), but higher than Gypsum (0.22).

Compost had a significant effect on average weight per seed ($p = 0.035$) and harvest index ($p = 0.014$), such that plants with compost added had lower average seed weight (16.9 mg seed⁻¹) and harvest index (0.45) compared to treatments without compost (18.5 mg seed⁻¹ and 0.49 for harvest index). Earthworms also had a significant effect, such that the number of seeds was 18.4% lower in treatments with earthworms ($p = 0.009$) and the harvest index showed a marginally significant decrease of 8.5% in the presence of earthworms ($p = 0.089$).

A significant compost by earthworm interaction suggested that the treatments with compost and earthworms had the lowest average seed weight ($p = 0.031$; Fig. 4A) and harvest index ($p = 0.049$; Fig. 4B) compared to other combinations. The average seed weight in treatments with both compost and earthworms was more than 10% lower relative to the other three soil treatments, while harvest index was more than 22% lower in treatments with both compost and earthworms added relative to the other three soil treatments.

Nitrogen Uptake and Grain Quality

Genotype demonstrated significant impacts on all plant N variables. The *Ae. tauschii* accession was lower for all N variables compared to the true wheat genotypes. At the same time, the older genotypes had higher total aboveground N uptake (0.244 g plant⁻¹) than modern genotypes (0.229 g plant⁻¹), but they allocated lower N to grain (0.42%) than modern genotypes

(0.46%). Compost increased total aboveground N uptake on average by 24.3%, but decreased the proportion of grain N uptake relative to total aboveground N uptake by 24.7%. Earthworms lowered total N uptake and the proportion of total N in the grain on average by 7.0% and 11.8%, respectively (Table 4).

Significant interactions of genotype x compost ($p = 0.011$) and genotype x earthworm ($p = 0.034$) were found for N uptake in the vegetative biomass. Compost increased vegetative biomass N uptake in all genotypes, and this was statistically significant for all genotypes except for Red Fife (Fig. 5A). The highest increases occurred in *Ae. tauschii* (102%), followed by modern genotypes Rht2M (81%) and Rht2W (58%). Older genotypes (Gypsum and Red Fife) increased the vegetative biomass N uptake in response to compost by 26% and 21% respectively. Earthworms decreased the vegetative biomass N uptake in Rht2W, but had no significant effect on the other genotypes (Fig. 5B). When examining total aboveground N uptake, a significant compost x genotype interaction ($p = 0.023$) indicated that the effect of compost depended on the genotype in question. Both *Ae. tauschii* and Rht2M showed a significant increase in N uptake with compost, but no significant effects were observed for the other genotypes (Fig. 5C).

Plants with compost additions had higher grain N concentration than without compost for Gypsum (0.37%), Red Fife (0.57%), Rht2M (0.14%), and Rht2W (0.14%), while in *Ae. tauschii*, it was lower by 0.36% (Fig. 6A). The proportion of grain N uptake relative to total aboveground biomass N uptake decreased with compost additions for *Ae. tauschii* (43%), Red Fife (26.4%), Rht2M (25%), and Rht2W (36%), but there were no significant effects on Gypsum (Fig. 6B). Earthworms decreased the proportion of grain N uptake relative to total aboveground biomass N uptake in *Ae. tauschii* (39%) and Gypsum (31%), while the effect was not significant in Red Fife, Rht2M, and Rht2W (Fig. 6C).

DISCUSSION

Overall, my hypothesis that older wheat genotypes would have a greater response to improved soil biological function (achieved via addition of compost and/or earthworms) relative to newer genotypes was not well supported by my findings. However, differences in above and belowground phenotypic traits emerged across genotypes and were related to how genotypes responded to soil improvements. Moreover, the multiple significant interactions between genotype and soil treatments for various plant growth parameters suggest that genotypic response is important to consider in the adoption of new management regimes that are likely to alter soil health. While the *Ae. tauschii* accession was generally the most responsive to soil conditions, important differences were also apparent among the *T. aestivum* genotypes (when wild accession was excluded from analysis).

Genotypic Effects on Plant Growth and Performance Traits

In considering the breeding history of *T. aestivum* genotypes and their evolution from wild ancestors (including *Ae. tauschii*), I expected to see strong divergences in phenotypic traits related to root growth and morphology and N uptake and allocation patterns. Specifically, I anticipated that *Ae. tauschii* would allocate more C towards root biomass relative to more modern genotypes that were bred in part for improved harvest index. *Ae. tauschii* and the modern genotypes represent the two bookends of historical gradient, where I would expect to see the largest differences in plant traits. However, the older landraces, Red Fife and Gypsum, should be less predictable in terms of their phenotypic traits given a less systematic breeding approach and likely differences in the selection environments and objectives between the two landraces. For example, Red Fife originated in the Ukraine where wheat cultivation practices differ

dramatically from Gypsum's Colorado origin. Indeed, for many of the above and belowground traits, Red Fife was more like modern genotypes, while Gypsum was more similar to the wild type.

Breeding programs focused on increasing harvest index and grain yield can result in lower vegetative and root biomass. For example, Feil (1992) and Bektas et al. (2016) showed significant phenotypic differences between landraces and modern wheat where landraces tended to have greater shoot biomass, total root biomass and number of tillers per plant compared to modern wheat. However, Crush et al. (2009) compared the root growth pattern of a wild population and bred perennial ryegrass and concluded that selection based on aboveground performance does not necessarily alter root systems, and better plant performance might result from an increase in root system size structure. In my study, both *Ae. tauschii* and Gypsum showed overall greater root biomass, higher root:shoot ratio, root length and average root diameter relative to modern genotypes. The larger root diameter of the wild accession was also found by Grossman and Rice (2012) in barley (*Hordeum spontaneum*). They postulated that the wild types has greater reliance on mycorrhizae, which can functionally substitute for root hairs, was the main factor of the thicker root in wild accession. Despite the greater investment in belowground C, higher aboveground biomass and tiller production was also observed in the wild *Ae. tauschii* compared to *T. aestivum* genotypes. This is in contrast with Wacker et al. (2002) who studied the trends of biomass fractionation in winter wheat and barley across domestication levels and found that the aboveground biomass per individual increased with domestication level. However, their analysis showed that the selection process did not alter the basic pattern of dry matter investment (in roots vs. leaves) from the wild ancestors.

In terms of yield, *Ae. tauschii* exhibited a typical wild type seed production strategy with large seed number, but low seed weight, leading to low yield. As expected, modern genotypes had higher yield, though not statistically significant compared to older genotypes. While modern genotypes have been bred, and cultivated under high inputs, the low fertilizer rate and compost treatment in this study were not likely to meet the nutrient demands for the modern genotypes to reach their potential yield.

Modern genotypes generally had lower grain N concentration than older genotypes. My finding is in accordance with Acreche and Slafer (2009) who found that grain N content decreased with the year of release of the genotypes. As grain N content depended strongly on the source-sink ratio at anthesis, namely between the number of grains set and the amount of N absorbed, modern genotypes that have high yield through increase in grain number may reduce the grain N content by diluting a limited source of N into more grains. A review by Feil (1992) explained that lower N content in modern genotypes may be due to the well-known tradeoff between grain yield and grain N concentration. Comparing the two modern genotypes, there was no significant difference in growth, yield and N uptake between Rht2M (contains *Rht-D1b* dwarf allele) and Rht2W (contains *Rht-D1a* tall allele). I found no differences in the grain quality, reflected by grain N concentrations, between modern genotypes despite previous studies indicating a decline in grain quality associated with semi-dwarf allele *Rht-D1* (Lanning et. al., 2012; Sherman et al., 2014). I note that the rootboxes used in my study provided a highly artificial environment that may yield inconsistencies with previous studies, though relative responses between genotypes are still likely to be relevant.

Though Gypsum and *Ae. tauschii* exhibited similar root traits, they diverged in their N uptake and allocation patterns. Gypsum had the highest grain N concentration and vegetative

biomass N uptake among all wheat genotypes, while *Ae. tauschii* exhibited the lowest N uptake in both vegetative and grain tissue. Gypsum also had the lowest harvest index, seed number, and proportion of total N allocated towards grain compared to all other wheat genotypes in the study. This is suggestive of greater investment towards vegetative growth rather than reproductive organs such as grain, a trait often associated with survivorship, conservation, and longevity and likely more typical in low-resource environments. For domesticated annual crop species, this characteristic may also be evident in landraces that are genetically closer to their wild ancestors.

It is certainly likely that the phenotypic differences I observed are a result of selection and breeding objectives, but I propose that some of the phenotypic differences across genotypic gradient are also related to where the genotypes fall along a resource economic spectrum. Underpinning plant community ecology is the theory that species fall along an axis of tradeoffs in resource acquisition strategies between fast and rapid uptake at the expense of resource conservation and longevity (Reich, 2014). Where a species falls along this axis can have important consequences for how nutrients are utilized by plants and may influence how plants respond to organic amendment additions (Martin and Isaac, 2015). Plant traits, including root traits, are often used to determine where species fall along this axis. Root diameter for example is often positively associated with slower resource uptake, but shorter root turnover and thus an indicator of a resource conservation strategy (Eissenstat, 1992; Kong et al., 2016). Though this has been widely demonstrated across species, it is less clear whether such resource acquisition tradeoffs exist within species and crop species (Martin and Isaac, 2015). In my study, both the wild accession and the landrace, Gypsum, exhibited key traits, such as greater root diameter, slower above ground growth (i.e. time to heading), and reduced N allocation to grain, that would be indicative of a resource conservation strategy relative to modern genotypes and Red Fife.

These results provide some initial evidence that a resource strategy spectrum could also exist across genotypes, which could have implications for both determining crop nutrient use as well as how crop genotypes respond to management practices.

Soil Improvement Effects on Plant Growth and Performance Traits

While some results point to phenotypic differences emerging due to genetic and evolutionary history, many of the traits measured vary with environmental conditions such as changes to biological activity and organic matter. Compost and manure amendments are a primary management strategy for providing plant nutrients in organic and low-input agricultural systems. Compost additions also improve physiochemical soil properties, as well as biological activity by providing substrate and nutrients for metabolism (Garcia et al., 2008). However, composted manure is typically less labile relative to raw manure and its effects on plant growth can be variable (Sommer, 2001; Preusch et al., 2002). Depending on the quality of the compost, there may be less N available for plant uptake from compost due to slow mineralization and N immobilization by soil microbes (Gagnon et al., 1997). Regardless of effects on plant nutrient uptake, compost amendments are a widely used and effective strategy for SOM accumulation and for building long-term soil health.

Compost additions yielded several important influences on plant growth in this study. Positive effects were observed for the number of tillers, root biomass and root length, but effects were not significant for aboveground biomass, yield, and root diameter. While compost generally increased vegetative N uptake, it did not affect grain N uptake leading to lower proportion of total N found in the grain. My findings are broadly in accordance with previous wheat studies

indicating that compost can lead to increased tiller production (Ibrahim et al., 2008), root and aboveground biomass (Keeling et al., 2003), and N uptake (Wang et al., 2016).

In general, the earthworm effect was erratic. While earthworms prolonged heading date, harvest index decreased, which is contrary to past research demonstrating enhanced crop yield through N mobilization (Van Groenigen et al., 2014). However, I also observed that earthworms decreased root diameter, which can be related to both root longevity as well as root absorption capacity (Eissenstat, 1992) and thus earthworms may be influencing plant nutrient acquisition strategies. Earthworms may alter root growth and morphology, not just through changes in soil N mobilization, but also through effects on soil physicochemical properties (Blanchart et al., 1999). For example, Canellas et al. (2002) linked root elongation and lateral root emergence to earthworm production of organic acids. The magnitude of earthworm effects on plant traits is influenced by several factors such as organic matter concentration, earthworm density, soil structure, and type and rate of fertilization, all of which likely influenced some of the observed plant responses to earthworms. While earthworms did generate some significant impacts, their poor survival in the rootboxes limits the inferences that can be drawn about the influence of earthworms on overall wheat growth and performance.

Interactive Effects on Plant Growth and Performance Traits

The wild wheat ancestor and older landraces were expected to exhibit stronger responses to compost and earthworm additions relative to modern genotypes, partly due to greater belowground C allocation that would: a) result in greater mineralization of organic inputs and thus nutrient uptake, and b) increase root access to nutrients. However, significant interactions between genotypes and soil treatments were inconsistent, such that I cannot conclude that there

is a linear relationship between genotype history and phenotypic response to soil management. Importantly though, I observed some interactions that suggest that genotype plasticity to compost and earthworm amendments depends on how certain traits like root diameter, root biomass and root:shoot ratio are initially expressed in the absence of soil amendments. For example, genotypes with overall higher root:shoot ratio also had the greatest response in their root:shoot ratio under compost additions. Thus, it can be suggested that, independent of genotype history, genotypes with certain phenotypic traits, may be more prone to adapting to improved soil environment.

Several observed interactions consistently show that the wild accession and Gypsum responded differently than modern genotypes to compost, especially in terms of root morphology and biomass. Root morphology can be plastic in response to many soil conditions, including nutrient status, aeration, temperature, physical impedance, and microorganism infection (Macduff et al., 1986; López-Bucio, 2003), though it may be that root plasticity depends in part on the genotype. In this study, I found that soils with organic nutrient additions increased root length, biomass, and diameter only in *Ae. tauschii* and to a lesser extent in Gypsum (Fig. 1D, 2A, 2B), indicating that they could adapt more readily to potential increases in soil biological activities. In natural environments with limited nutrient inputs, wild accessions and older genotypes may have adapted to invest more in root systems to be able to access nutrients and upregulate biological nutrient mineralization (Schmidt et al., 2016). Modern genotypes, on the other hand, exhibited little root trait plasticity except in root diameter. Interestingly, the direction of the response was opposite to the wild species and Gypsum, where root diameter decreased with compost. This corresponds to a nutrient and water acquisition strategy that favors rapid uptake and growth over conservation (Eissenstat, 1992). This type of strategy is also reflected in

the stable root length, but lower average diameter observed in the modern genotypes with compost additions (Fig. 2B).

In comparing the two-near isogenic modern genotypes, I found that Scholar Rht2M (semi-dwarf) and Scholar Rht2W behaved similarly in root morphology in response to compost addition. This suggests little effect of the dwarf allele on root growth responses to organic matter. My result was in line with Cholick et al. (1977) who found that plant height had no significant relationships to rooting depth or moisture extraction patterns under dryland field conditions in eastern Colorado. However, other studies indicated that the semi-dwarf gene can affect root systems. The tall genotypes had lower root number, longest root length, and total root length than the semi-dwarf genotypes in a study by Li et al. (2011). Despite the strong interactions between genotype and compost with root traits in this study, the response in aboveground biomass, N uptake and allocation were not consistent with what would be expected with greater biological activity and enhanced root growth. I also note that the aboveground responses to compost observed here were far more muted compared to the root responses.

Red Fife was the only wheat genotype affected by compost in terms of aboveground biomass and this was a negative response (Fig. 1C, 1E). Red Fife also exhibited a negative response to compost in terms of grain N uptake, seed weight and yield, resulting in several contrasting effects of compost between Gypsum and Red Fife. While Gypsum had a similar response to the wild accession with compost, Red Fife tended to respond more like the modern genotypes. It appears the landrace more associated with lower root biomass, root:shoot ratio, and root diameter in the control (no compost, no earthworm) is also inhibited by organic inputs. It is possible that low belowground investment by Red Fife fosters lower total biological activity and turnover, and thus more N is immobilized with compost in Red Fife relative to other genotypes

with greater belowground inputs. The differences in interactions I observed between the two landraces may also be artefacts of breeding and cultivation history that can have critical effects on the landraces' ability to interact with soil biological activity.

Gypsum, originating from Colorado, may have been adapted to Colorado's soil characterized by relatively arid conditions and low nutrient inputs, such that under an improved environment (i.e. sufficient moisture and compost), it responded positively perhaps because of some conserved root traits. I suspect that Red Fife, initially from Western Ukraine (Symko, 2002) was cultivated under a context of greater inputs and better growing conditions given that Europe has traditionally invested more resources into wheat cultivation and set aside some of its most fertile soils for wheat, long the most important commodity crop in Europe (Litvinenko et al., 2001). Thus, Red Fife may lack the strong historical relationship with Colorado soil (and associated conditions), so that it has limited response to soil amendments. These differences indicate the importance of knowing the evolutionary and cultivation history related to the plant x soil interactions.

Different from all the cultivated genotypes, *Ae. tauschii*, showed a significant increase in aboveground biomass with compost. Differential resource allocation in aboveground biomass between ancient and modern maize in response to N adequacy was compared by Gaudin et al. (2011). They suggested that the maize ancestor increased allocation towards more tillers and leaf production whereas, modern genotypes increased leaf size and stem weight. In my study, the longer time *Ae. tauschii* grew in the greenhouse to reach maturity may have contributed to the higher aboveground biomass.

There was a tendency to increase N uptake in some genotypes with compost addition (*Ae. tauschii* and Rht2M), but the proportion allocated to grain declined in all genotypes except

Gypsum (Fig. 6B). The low allocation of N to the grain may be the main factor causing insignificant compost effect on yield. In respect to the end-use quality, I found that compost generally had a positive impact on grain N concentration, an important variable related to protein content. Although only significant in Red Fife, the compost tended to increase grain N concentration (Fig. 6A). My result is in contrast with Pourazari et al. (2015) who compared growth and yield of the ancient and modern wheat genotypes under different fertilizer levels. While modern genotypes produced higher grain yield regardless of fertilization level, they found that grain N concentration was generally lower compared to the ancient genotypes. Though many breeding programs aim to increase grain quality under conventional management system, high baking quality traits under organic conditions were not adequately addressed (Osman et al., 2016). Therefore, they recommend development of spring wheat genotypes that have high baking quality and are better adapted to organic management systems.

The only significant genotype x earthworm interactions were found for vegetative biomass N uptake and proportion of grain N uptake to total aboveground N uptake (Fig. 5B, 6C). My result is in contrast to Noguera et al. (2011) who showed the positive interaction effect of genotype and earthworm, such that the presence of earthworm increased shoot:root ratio, grain biomass, and total biomass. However, my results are partially supported in a previous study by Stephens et al. (1994) that found that earthworms caused a significant negative effect on foliar concentrations of elements including N.

Implications for Genotype Selection under Improved Soil Health

Findings from my work suggest that the wild accession and landrace, Gypsum, responded positively to organic matter inputs, more so than modern genotypes. However, the other

landrace, Red Fife, often produced an opposing response to compost amendments. Thus, the evolutionary history of domestication and cultivation may be a crucial factor to consider when targeting genotypes that can best facilitate beneficial plant-soil feedbacks. The ancestor *Ae. tauschii*, and older genotype Gypsum, exhibited lower yields and harvest index, though grain N concentration, a proxy for protein content and grain quality, was highest in Gypsum relative to other genotypes. This may be a beneficial trait for certain markets as wheat genotypes are increasingly being sought for their bread making quality, especially by artisan bread makers and small farmers (Mader et al., 2007; Di Silvestro et al., 2012). More broadly, yielding less may also come with several beneficial traits that are worth considering in breeding efforts. For example, with growing initiatives to incorporate more sustainable practices into agroecosystems, it will be important to choose genotypes that are responsive to SOM accrual and overall soil health improvement. Moreover, genotypes such as Gypsum, with greater root biomass and root length may encourage more soil C sequestration, reduced soil nitrate leaching into groundwater, and improvements to soil structure and water infiltration (Angers and Caron, 1998; Ehdaie et al., 2010; Kell, 2011).

In terms of promoting beneficial plant-soil interactions, Gypsum suggested a more positive response to compost addition in some traits related to aboveground and root biomass, indicating that this genotype may benefit more from soil health promoting practices. In turn, greater aboveground biomass may benefit soil organisms through greater C returns to the soil via crop residues (Collins et al., 1992; Hoyle and Murphy, 2011). Moreover, greater root systems likely have higher root exudation, which encourages plant-soil interactions related to disease suppression, nutrient acquisition and protection against abiotic stressors (Szoboszlay et al., 2015). Ancestral and landrace crops can be a valuable resource in breeding (Bektas et al., 2016)

to improve modern genotypes (Dwivedi et al., 2016). For example, wild relatives have been used as a genetic source for drought and salinity tolerance traits (Nevo and Chen, 2010; Budak et al., 2013). Thus, I propose that greater exploration of belowground traits in ancient and older genotypes could help to reinstate the benefits of plant x soil biological interactions under conditions of improving soil health. If we expand our research efforts of linking plant traits with resource acquisition strategies in cultivated annual crops we may also begin to better predict and identify which crop genotypes will exhibit greater nutrient uptake and performance in a context of improving soil health.

To identify and breed genotypes that can take benefits from plant-soil interactions, breeding strategies for specific intention such as organic and low-input system could be adopted. A review by Wolfe et al. (2008) suggests three breeding approaches for organic and low-input wheat production: 1) Selection under conventional farming conditions, followed by testing and selection for ones that perform well under organic or low-input conditions; 2) Genotypes initially derived from conventional breeding programs are later bred for new generations screened and selected under organic conditions, and; 3) Breeding programs focus on organic demanded traits and is carried out in organic farming conditions from the initial stage. Murphy et al. (2007) suggested that this last direct selection approach within organic or low-input agroecosystem is more reliable rather than indirect selection in conventional farming systems. Breeding for organic nutrients and soil biological activity improvement should be carried out in corresponding environments.

CONCLUSION

In this study, I observed notable differences among wheat genotypes in their response to increased soil fauna activity and organic amendments. For several phenotypic traits (e.g., root length, average root diameter), the ancestor and the older Gypsum genotype tended to have greater responses to organic matter addition. The genotypes that have historical breeding and management contexts associated with lower inputs and a greater reliance on organic nutrient sources appear to exhibit greater plasticity in their response to organic matter inputs and associated changes in soil biological activity. While my findings do not provide strong evidence for the hypothesis that older genotypes would respond better to organic inputs and improved soil biological activity, my results suggest that different genotypes can perform distinctly in conditions of improved soil health and this should be considered within future breeding objectives.

RECOMMENDATIONS

1. Wild ancestors and older genotypes should be considered as source material for breeding programs since they may have beneficial traits for taking advantage of improved soil health and associated plant-soil organism interactions.
2. Direct breeding approaches within conditions of enriched soil organic matter and active soil fauna populations is recommended for selecting genotypes are adapted and can best take advantage of conditions of improved soil health.

TABLES

Table 1. Means for plant growth and biomass variables for *Ae. tauschii* and four spring wheat genotypes grown in the greenhouse under differing soil treatments.

Treatment	Heading date (days)	Number of tillers (tillers plant ⁻¹)	Above-ground biomass (g plant ⁻¹)	Root biomass (g plant ⁻¹)	Total biomass (g plant ⁻¹)	Root:shoot Ratio
<i>Ae. tauschii</i>						
NC-NE	104.4 ± 1.7	36.0 ± 1.0	11.5 ± 0.1	1.62 ± 0.16	13.1 ± 0.2	0.140 ± 0.013
NC-E	108.2 ± 1.0	34.4 ± 3.7	9.5 ± 0.4	1.14 ± 0.10	10.6 ± 0.4	0.121 ± 0.010
C-NE	113.0 ± 2.7	59.8 ± 4.7	16.9 ± 2.2	2.85 ± 0.60	19.7 ± 2.7	0.163 ± 0.016
C-E	120.0 ± 1.5	69.7 ± 6.4	16.8 ± 4.5	4.27 ± 2.72	21.1 ± 7.2	0.212 ± 0.085
Gypsum						
NC-NE	49.6 ± 1.0	13.0 ± 1.6	10.9 ± 1.4	0.57 ± 0.12	11.5 ± 1.5	0.050 ± 0.005
NC-E	51.0 ± 2.1	15.0 ± 1.6	10.5 ± 0.9	0.56 ± 0.09	11.0 ± 1.0	0.052 ± 0.005
C-NE	49.8 ± 1.4	15.0 ± 1.1	13.0 ± 1.4	0.68 ± 0.07	13.7 ± 1.5	0.052 ± 0.001
C-E	52.0 ± 1.9	16.2 ± 1.4	11.5 ± 0.7	0.80 ± 0.09	12.3 ± 0.7	0.069 ± 0.005
Red Fife						
NC-NE	44.6 ± 0.5	15.6 ± 1.2	10.0 ± 0.3	0.31 ± 0.02	10.3 ± 0.3	0.031 ± 0.002
NC-E	46.6 ± 0.8	16.6 ± 1.5	11.2 ± 1.0	0.46 ± 0.04	11.6 ± 1.0	0.041 ± 0.003
C-NE	47.2 ± 1.3	13.6 ± 1.4	7.4 ± 0.9	0.30 ± 0.08	7.7 ± 1.0	0.038 ± 0.006
C-E	45.0 ± 1.0	13.2 ± 2.8	7.5 ± 2.0	0.27 ± 0.12	7.8 ± 2.1	0.031 ± 0.006
Rht2W						
NC-NE	44.2 ± 1.3	14.8 ± 0.8	11.4 ± 0.6	0.47 ± 0.05	11.8 ± 0.7	0.041 ± 0.003
NC-E	44.8 ± 1.6	9.2 ± 0.9	8.6 ± 0.5	0.31 ± 0.03	8.9 ± 0.5	0.036 ± 0.003
C-NE	46.5 ± 2.2	10.3 ± 1.7	9.6 ± 1.2	0.39 ± 0.06	10.0 ± 1.2	0.041 ± 0.006
C-E	46.4 ± 1.3	13.4 ± 0.8	7.6 ± 1.6	0.28 ± 0.06	7.9 ± 1.6	0.037 ± 0.002
Rht2M						
NC-NE	45.2 ± 0.7	12.0 ± 2.2	8.2 ± 1.5	0.35 ± 0.06	8.6 ± 1.5	0.043 ± 0.003
NC-E	43.6 ± 1.0	13.2 ± 1.9	10.3 ± 0.8	0.41 ± 0.06	10.7 ± 0.9	0.040 ± 0.002
C-NE	44.2 ± 0.5	13.6 ± 0.7	10.4 ± 1.3	0.39 ± 0.04	10.8 ± 1.3	0.038 ± 0.001
C-E	46.6 ± 1.2	14.8 ± 1.3	9.7 ± 1.8	0.36 ± 0.10	10.0 ± 1.9	0.034 ± 0.004
Analysis of Variance						
Source						
G	***	***	***	***	***	***
C	***	***	ns	*	ns	Ns
E	*	ns	ns	ns	ns	Ns
G x C	**	***	***	**	***	*
G x E	ns	ns	ns	ns	ns	Ns
G x E	ns	ns	ns	ns	ns	Ns
V x G x E	ns	ns	ns	ns	ns	Ns

NC-NE, no compost or earthworms added; NC-E, no compost, but earthworms added; C-NE, compost added, no earthworms; C-E, both compost and earthworms added. Standard errors are presented to the right of each mean. ANOVA results are located at the bottom with significance indicated (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant) for all experimental factors and interactions (G, genotype; C, compost; E, earthworm).

Table 2. Means for root length and average root diameter for *Ae. tauschii* and four spring wheat genotypes grown in the greenhouse under differing soil treatments.

Treatment	Root length (m plant ⁻¹)	Average root diameter (mm)
<i>Ae. tauschii</i>		
NC-NE	378.2 ± 49.6	0.96 ± 0.13
NC-E	228.7 ± 26.6	0.73 ± 0.04
C-NE	681.5 ± 191.6	1.40 ± 0.24
C-E	616.4 ± 268.2	1.08 ± 0.30
Gypsum		
NC-NE	130.9 ± 26.9	0.53 ± 0.01
NC-E	125.1 ± 20.3	0.54 ± 0.02
C-NE	154.0 ± 23.3	0.53 ± 0.01
C-E	219.7 ± 45.9	0.53 ± 0.03
Red Fife		
NC-NE	76.2 ± 8.7	0.53 ± 0.01
NC-E	120.0 ± 8.6	0.52 ± 0.01
C-NE	76.1 ± 28.1	0.56 ± 0.02
C-E	79.1 ± 39.6	0.31 ± 0.05
Rht2W		
NC-NE	100.0 ± 12.7	0.55 ± 0.02
NC-E	66.7 ± 10.9	0.55 ± 0.02
C-NE	113.2 ± 22.9	0.53 ± 0.03
C-E	66.6 ± 29.7	0.29 ± 0.06
Rht2M		
NC-NE	78.4 ± 16.6	0.56 ± 0.02
NC-E	78.1 ± 12.5	0.56 ± 0.02
C-NE	90.5 ± 11.8	0.53 ± 0.02
C-E	100.2 ± 32.2	0.37 ± 0.05
Analysis of Variance		
Source		
G	***	***
C	*	Ns
E	ns	***
G x C	**	***
G x E	ns	Ns
C x E	ns	***
G x C x E	ns	Ns

NC-NE, no compost or earthworms added; NC-E, no compost, but earthworms added; C-NE, compost added, no earthworms; C-E, both compost and earthworms added. Standard errors are presented to the right of each mean. ANOVA results are located at the bottom with significance indicated (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant) for all experimental factors and interactions (G, genotype; C, compost; E, earthworm).

Table 3. Means for yield variables for *Ae. tauschii* and four spring wheat genotypes grown in the greenhouse under differing soil treatments.

Treatment	Number of seeds (seeds plant ⁻¹)	Seed weight (g plant ⁻¹)	Average weight per seed (mg seed ⁻¹)	Harvest index
<i>Ae. tauschii</i>				
NC-NE	252.8 ± 5.2	1.11 ± 0.04	4.38 ± 0.17	0.096 ± 0.004
NC-E	154.0 ± 28.5	0.66 ± 0.15	4.04 ± 0.37	0.067 ± 0.014
C-NE	275.8 ± 42.0	1.25 ± 0.29	4.37 ± 0.37	0.076 ± 0.014
C-E	206.0 ± 118.3	1.05 ± 0.86	3.40 ± 1.49	0.046 ± 0.032
Gypsum				
NC-NE	116.5 ± 15.5	2.70 ± 0.43	22.91 ± 1.82	0.243 ± 0.016
NC-E	101.8 ± 27.1	2.25 ± 0.63	22.04 ± 1.13	0.204 ± 0.048
C-NE	152.8 ± 21.3	3.35 ± 0.36	22.72 ± 2.46	0.259 ± 0.013
C-E	98.4 ± 11.4	1.96 ± 0.19	20.35 ± 1.42	0.170 ± 0.011
Red Fife				
NC-NE	126.8 ± 9.9	2.90 ± 0.23	23.04 ± 1.22	0.290 ± 0.021
NC-E	136.8 ± 15.2	3.36 ± 0.56	24.35 ± 1.79	0.295 ± 0.024
C-NE	82.0 ± 9.6	1.95 ± 0.29	23.73 ± 1.51	0.264 ± 0.022
C-E	104.2 ± 35.8	2.00 ± 0.57	20.45 ± 1.60	0.254 ± 0.028
Rht2W				
NC-NE	169.6 ± 5.5	3.47 ± 0.32	20.63 ± 2.30	0.303 ± 0.015
NC-E	124.8 ± 13.8	2.78 ± 0.36	22.46 ± 2.63	0.320 ± 0.034
C-NE	145.5 ± 21.1	2.99 ± 0.50	20.57 ± 1.88	0.309 ± 0.029
C-E	93.6 ± 39.2	1.91 ± 0.84	18.17 ± 1.70	0.200 ± 0.068
Rht2M				
NC-NE	144.0 ± 28.4	2.71 ± 0.59	18.36 ± 1.00	0.318 ± 0.021
NC-E	167.2 ± 11.5	3.81 ± 0.46	23.12 ± 3.06	0.369 ± 0.036
C-NE	193.6 ± 32.9	3.52 ± 0.63	18.17 ± 0.61	0.333 ± 0.022
C-E	167.8 ± 37.9	3.06 ± 0.83	17.31 ± 1.42	0.296 ± 0.034
ANOVA				
Source				
G	***	***	***	***
C	ns	ns	*	*
E	**	ns	ns	**
G x C	ns	ns	ns	ns
G x E	ns	ns	ns	ns
C x E	ns	ns	*	*
G x C x E	ns	ns	ns	ns

NC-NE, no compost or earthworms added; NC-E, no compost, but earthworms added; C-NE, compost added, no earthworms; C-E, both compost and earthworms added. Standard errors are presented to the right of each mean. ANOVA results are located at the bottom with significance indicated (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant) for all experimental factors and interactions (G, genotype; C, compost; E, earthworm).

Table 4. Means for nitrogen concentration and uptake for *Ae. tauschii* and four spring wheat genotypes grown in the greenhouse under differing soil treatments.

Treatment	Vegetative biomass N concentration (%)	Grain N concentration (%)	Vegetative biomass N uptake (mg plant ⁻¹)	Grain N Uptake (mg plant ⁻¹)	Total above-ground N uptake (mg plant ⁻¹)	Proportion of grain N uptake to total above-ground N uptake (g g ⁻¹)
<i>Ae. tauschii</i>						
NC-NE	0.49 ± 0.02	3.54 ± 0.07	56.0 ± 2.5	39.2 ± 1.3	95.1 ± 3.0	0.41 ± 0.01
NC-E	0.75 ± 0.12	3.77 ± 0.11	69.6 ± 8.0	24.2 ± 5.3	93.8 ± 4.0	0.26 ± 0.06
C-NE	0.74 ± 0.07	3.29 ± 0.23	119.0 ± 5.1	41.0 ± 9.1	160.0 ± 11.6	0.25 ± 0.04
C-E	0.89 ± 0.16	3.31 ± 0.40	135.1 ± 8.4	28.2 ± 21.4	163.2 ± 29.4	0.12 ± 0.09
Gypsum						
NC-NE	1.26 ± 0.07	4.20 ± 0.20	137.2 ± 20.8	110.8 ± 14.3	248.0 ± 33.5	0.45 ± 0.02
NC-E	1.45 ± 0.05	3.93 ± 0.27	146.8 ± 12.0	84.7 ± 21.8	223.5 ± 34.1	0.31 ± 0.06
C-NE	1.24 ± 0.14	4.20 ± 0.09	164.7 ± 30.6	141.0 ± 16.6	305.7 ± 44.8	0.47 ± 0.03
C-E	1.67 ± 0.02	4.68 ± 0.19	192.4 ± 11.5	91.5 ± 8.5	283.8 ± 19.9	0.32 ± 0.01
Red Fife						
NC-NE	1.00 ± 0.05	3.83 ± 0.25	100.1 ± 5.6	109.0 ± 4.2	209.1 ± 8.1	0.52 ± 0.01
NC-E	1.09 ± 0.15	3.72 ± 0.11	119.3 ± 14.6	122.6 ± 15.6	242.0 ± 17.7	0.50 ± 0.05
C-NE	1.83 ± 0.15	4.20 ± 0.03	133.8 ± 14.8	82.3 ± 12.8	216.1 ± 23.2	0.38 ± 0.03
C-E	1.84 ± 0.10	4.49 ± 0.15	132.0 ± 27.5	89.6 ± 26.4	221.5 ± 53.9	0.38 ± 0.03
Rht2W						
NC-NE	1.00 ± 0.08	3.68 ± 0.09	113.2 ± 11.1	126.8 ± 10.3	240.1 ± 18.5	0.53 ± 0.02
NC-E	0.86 ± 0.10	3.42 ± 0.17	73.5 ± 8.7	93.3 ± 10.0	166.8 ± 13.6	0.56 ± 0.04
C-NE	1.68 ± 0.07	3.47 ± 0.13	162.8 ± 22.8	104.7 ± 18.7	267.8 ± 38.3	0.39 ± 0.04
C-E	1.90 ± 0.31	4.50 ± 0.45	132.5 ± 24.2	73.7 ± 30.2	206.2 ± 51.2	0.30 ± 0.09
Rht2M						
NC-NE	1.28 ± 0.24	3.58 ± 0.27	95.0 ± 11.7	92.4 ± 17.3	187.4 ± 26.2	0.48 ± 0.04
NC-E	0.80 ± 0.12	3.44 ± 0.27	81.0 ± 9.9	126.3 ± 7.6	207.3 ± 10.9	0.61 ± 0.04
C-NE	1.64 ± 0.12	3.64 ± 0.04	165.2 ± 11.8	128.9 ± 24.4	294.1 ± 34.2	0.43 ± 0.03
C-E	1.63 ± 0.16	3.67 ± 0.17	152.4 ± 22.3	107.9 ± 25.9	260.2 ± 44.8	0.40 ± 0.04
ANOVA						
Source						
G	***	***	***	***	***	***
C	***	*	***	ns	***	***
E	ns	ns	ns	ns	ns	*
G x C	***	*	*	ns	*	*
G x E	*	ns	*	ns	ns	*
C x E	ns	*	ns	ns	ns	ns
G x C x E	ns	ns	ns	ns	ns	ns

NC-NE, no compost or earthworms added; NC-E, no compost, but earthworms added; C-NE, compost added, no earthworms; C-E, both compost and earthworms added. Standard errors are presented to the right of each mean. ANOVA results are located at the bottom with significance indicated (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant) for all experimental factors and interactions (G, genotype; C, compost; E, earthworm).

FIGURES

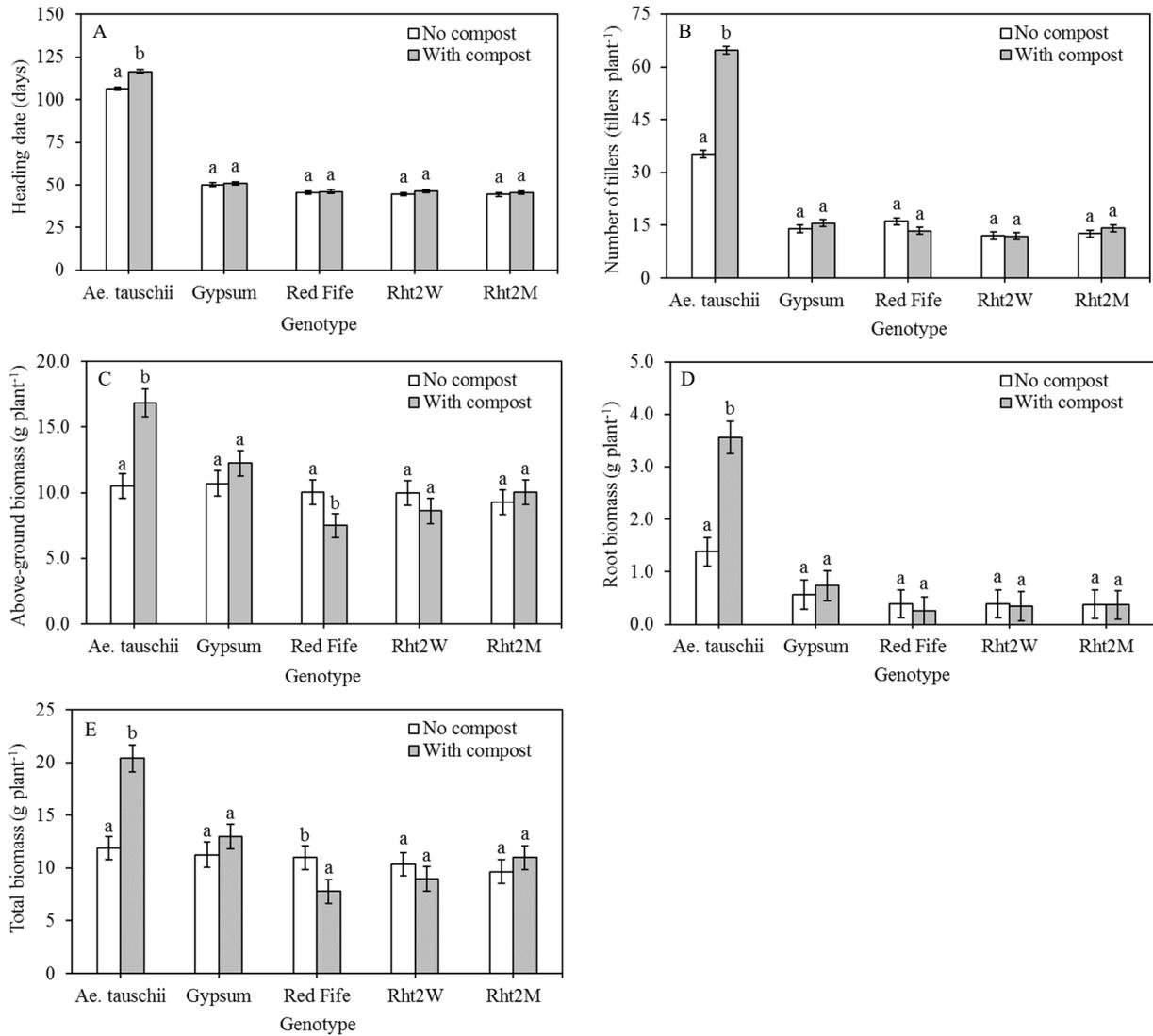


Figure 1. Comparison of compost effects for *Ae. tauschii* and four spring wheat genotypes grown in the greenhouse. Variables include: heading date (A), number of tillers (B), aboveground biomass (C), root biomass (D), total biomass (E). Error bars represent standard error. Bars with the same letter for each genotype indicate no significant difference based on Tukey comparison ($\alpha = 0.05$).

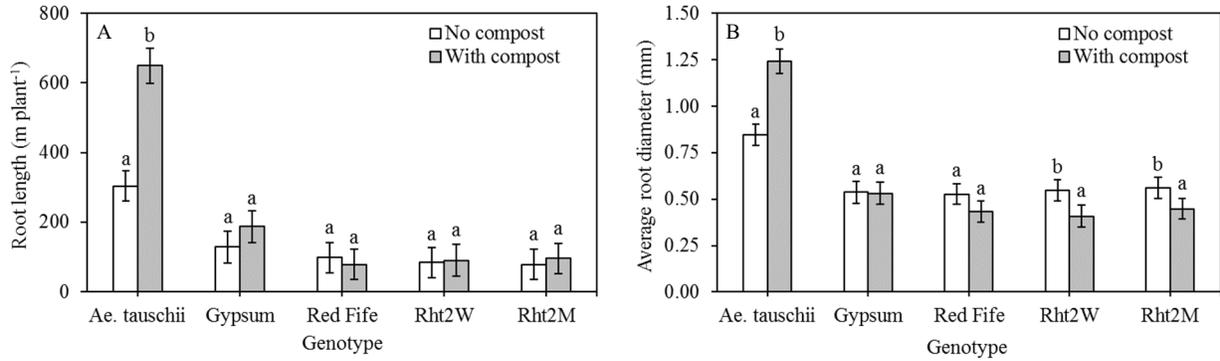


Figure 2. Comparison of compost effects for *Ae. tauschii* and four spring wheat genotypes grown in the greenhouse. Variables include: root length (A), average root diameter (B). Error bars represent standard error. Bars with the same letter for each genotype indicate no significant difference based on Tukey comparison ($\alpha = 0.05$).

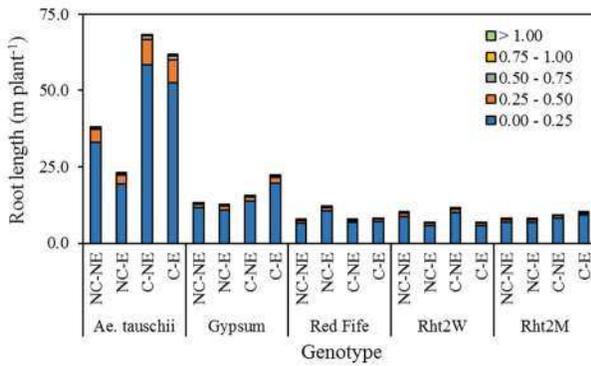


Figure 3. Root length per diameter class (0.00–0.25, 0.25–0.50, 0.50–0.75, 0.75–1.00, >1.00 mm). NC-NE, no compost or earthworms added; NC-E, no compost, but earthworms added; C-NE, compost added, no earthworms; C-E, both compost and earthworms added.

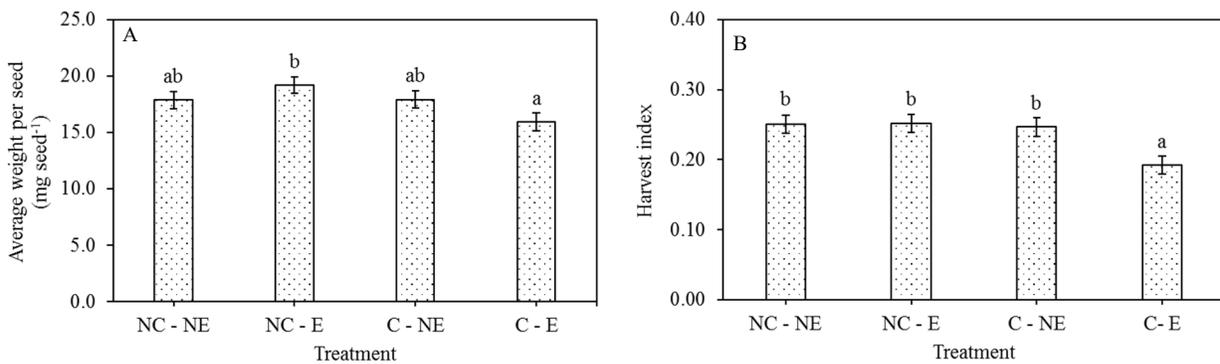


Figure 4. Comparison for interaction effects of compost x earthworm. Variables include: average weight per seed (A), harvest index (B). Error bars represent standard error. Bars with the same letter for each genotype indicate no significant difference based on Tukey comparison ($\alpha = 0.05$). NC-NE, no compost or earthworms added; NC-E, no compost, but earthworms added; C-NE, compost added, no earthworms; C-E, both compost and earthworms added.

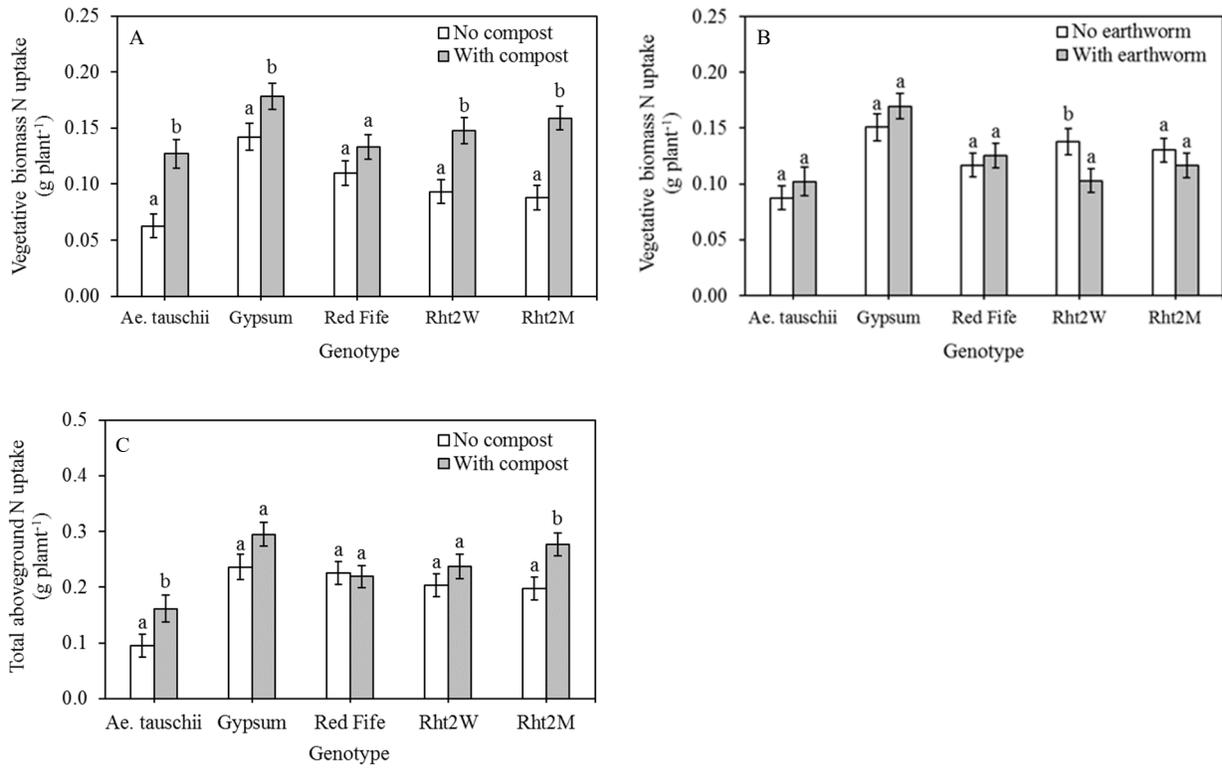


Figure 5. Comparison of compost (A) and earthworm (B) effects on vegetative N uptake, and compost effects on total aboveground N uptake (C) for *Ae. tauschii* and four spring wheat genotypes grown in the greenhouse. Error bars represent standard error. Bars with the same letter for each genotype indicate no significant difference based on Tukey comparison ($\alpha = 0.05$).

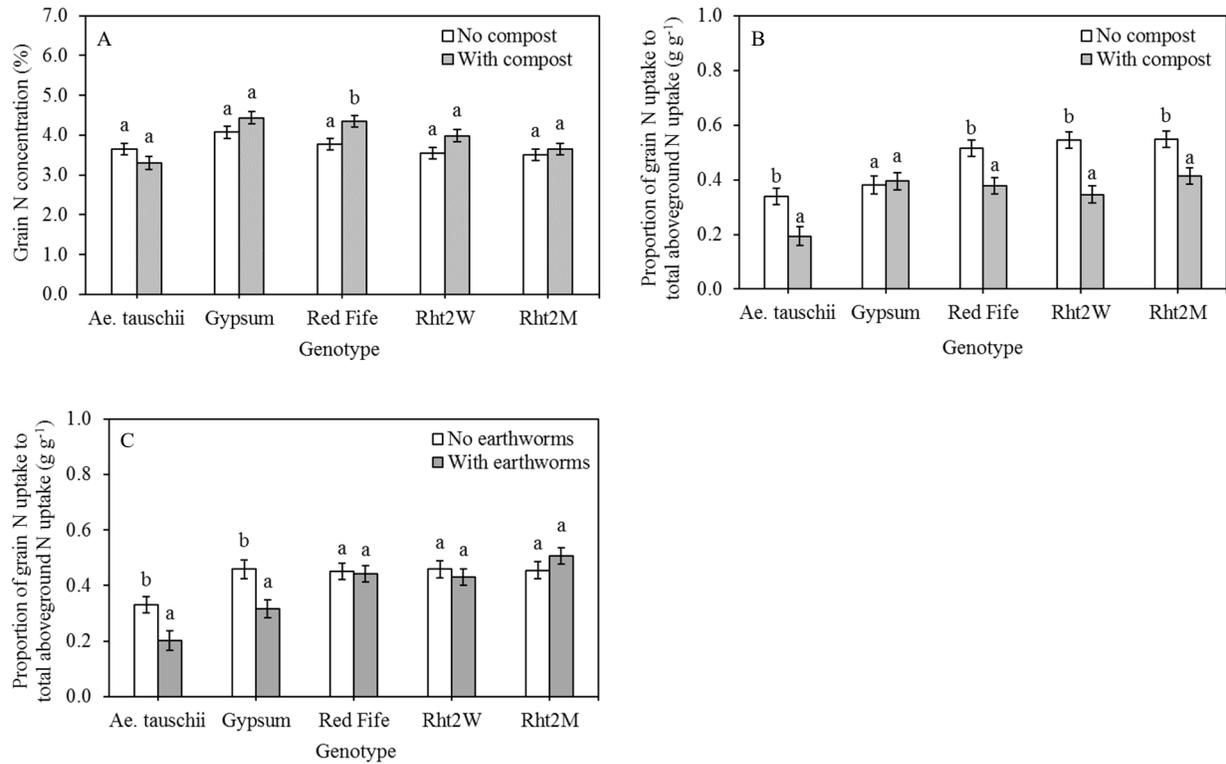


Figure 6. Comparison of compost effects on grain N concentration (A), proportion of grain N uptake to total aboveground N uptake (B), and earthworm effect on proportion of grain N uptake to total aboveground N uptake (C) for *Ae. tauschii* and four spring wheat genotypes grown in the greenhouse. Error bars represent standard error. Bars with the same letter for each genotype indicate no significant difference based on Tukey comparison ($\alpha = 0.05$).

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