

COMPOSTED DAIRY MANURE AND ARBUSCULAR MYCORRHIZAE INFLUENCE ON
WEED COMPETITION AND POTATO YIELD

By

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ABSTRACT

COMPOSTED DAIRY MANURE AND ARBUSCULAR MYCORRHIZAE INFLUENCE ON WEED COMPETITION AND POTATO YIELD

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Potatoes are an important global food crop typically produced in high-input systems in temperate zones. Growers that have access to compost may use it to improve soil health and increase tuber yields, but compost may also impact microbial communities, weed competition, weed seed fecundity, mortality, and dormancy. Potatoes were grown in field plots amended with 0, 4, or 8 t carbon (C) ha⁻¹ of compost during the summer under weed-free conditions, and in competition with common lambsquarters (CHEAL), giant foxtail (SETFA), and hairy nightshade (SOLSA). In the fall, one hundred seeds of each weed species from each of the composted field plots were buried to a 5-cm depth in the weed-free plots of each compost rate to measure mortality. Seed bags were removed 9 months after burial. Compost did not increase biomass, seed production, initial seed viability, or seed dormancy of any weed species. SETFA and SOLSA at five plants per meter of row reduced potato yield 20%; CHEAL reduced yield by 45%. Potato yield increased 5-15% in compost compared to non-compost treatments possibly due to elevated soil potassium levels. Burial environment did not affect seed survival within a species. As the compost rate in the maternal environment increased, seed mortality of SOLSA decreased, SETFA increased, and CHEAL was unchanged. Seed dormancy was unaffected by maternal and burial environment. Arbuscular mycorrhizal fungi (AMF) inoculum did not affect growth of potato, CHEAL, SETFA, or SOLSA in the greenhouse. Nutrient concentration in above-ground plant biomass varied by species, and was not affected by AMF inoculum. Nutrient use efficiency may affect weed competitiveness in nutrient-limited potato production systems.

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CHAPTER 1

Literature Review

Potatoes. Potato (*Solanum tuberosum* L.) is a perennial crop grown globally as an important food source. Underground stems, referred to as tubers, are produced by the plant and harvested for food. Annual world production of potatoes is around 300 million tonnes (t) (FAOSTAT 2011), and average annual United States production is over 36 million t, yielding 35 t ha^{-1} , with a market value of over 3 billion dollars (USDA-NASS 2011). Potatoes are grouped into market classes including russet, long white, round white, red, yellow, blue and purple, and fingerlings (USPB 2011b). Each class contains varieties or cultivars that produce similar tubers, but may have differing plant characteristics (i.e., plant architecture, maturity, and disease tolerance). Yield potential is also variety-dependent (Stark and Westermann 2008).

Five potato growth stages have been identified by researchers (Govindakrishnan and Haverkort 2006; Miller and Hopkins 2008). The first stage involves sprout development from the seedpiece. Sprouts and roots begin to emerge from meristematic tissue located on the tuber. Sprout initiation will occur when growing degree days (GDD) accumulate above 4°C (Allen and O'Brien 1986; Hartz and Moore 1978). Optimum soil temperature for emergence is 20 to 24°C , with temperatures outside this range slowing emergence. Adequate soil moisture is also necessary for root establishment and shoot emergence. The second stage involves vegetative growth and initiation of photosynthesis. Stem tissue develops into vines that produce leaves. If grown under high day and low night temperatures stem elongation occurs, whereas high night

temperatures promote branching. Temperature, water availability, and nutrients can impact leaf expansion. Plants are also producing stolons (underground stems) and roots underground.

The third stage, which lasts 10 to 14 days, is when tubers form at the tips of the stolons (called tuber initiation). This stage typically ends when the potato vines produce flowers, but temporal overlap may occur with tuber initiation and flowering. Tuber initiation is controlled by plant hormones, soil moisture, air and soil temperature, day length, and nitrogen (N) levels in the plant and soil. Low night temperatures are needed for tuber initiation, and if air temperature increases above 21°C, tuber initiation decreases. Early-maturing varieties require nutrient applications during the vegetative and tuber initiation stages, whereas late-maturing varieties need nutrient applications during the fourth stage, which is the bulking phase.

During the tuber bulking stage, tubers accumulate nutrients, photosynthate, and water. The tubers become the dominant sink, and vegetative aboveground growth slows drastically. Bulking begins slowly, increases to a constant rate, and then slows as the potato vines senesce. The duration of this stage is critical to photosynthate and tuber biomass accumulation. The rate of nutrient and carbohydrate translocation is also temperature dependent. Phloem-mobile nutrients, such as N, phosphorus (P), potassium (K), magnesium (Mg), and chlorine (Cl) are transported from the vines to tubers and follow an accumulation pattern similar to that of biomass accumulation (Stark and Westermann 2008). Non-mobile nutrients in the phloem, like calcium (Ca), sulfur (S), zinc (Zn), boron (B), manganese (Mn), and iron (Fe), accumulate in foliage during tuber growth and are not as affected by tuber demands. The final stage is maturation when the vines senesce, maximum tuber weight is attained, and tuber skin hardens.

Varieties can be determinate, meaning the potato plant will naturally mature and senesce, or indeterminate, and will continue to produce aboveground vegetative tissue until conditions

become conducive for tuber initiation and bulking. A determinate variety will experience peak dry foliage and root production at or before the midpoint of tuber growth and will decrease after this (Stark and Westermann 2008). Indeterminate varieties will delay tuber bulking during the bulking phase and produce more foliage and roots if there is high nitrogen availability. Applying the entire season N requirements preplant can delay tuber growth phase by 2 wk. Determinate varieties will develop more rapidly than indeterminate varieties (earlier canopy closure, causes earlier tuber growth). Indeterminate varieties will devote more energy to tuber production under N deficient conditions.

The determinate variety ‘Snowden’ produces round white potatoes and is commonly grown in Michigan for chip production. It is classified as a high yielding, late (110-130 days) maturing variety (CFIA 2011; USPB 2011a), but has shown variable response to N fertilizers (Long et al. 2004). Tubers have high specific gravity (Douches et al. 1996), a measure of tuber density, with short dormancy and storage potential. The variety was developed in 1990 with variable genetic parentage (Love 1999).

All of the nutrients accumulated by the plants are essential to various physical and physiological processes. N can increase the leaf area index (Perumal and Sahota 1986) and delay vine senescence (Santeliz and Ewing 1981). N application also delays tuber initiation, but dry matter accumulation and a longer period of vine vigor provide an extended bulking period to compensate for the delay in maturation (Biemond and Vos 1992). However, other researchers did not see a strong correlation with vine vigor and yield (Douds et al. 2007; Sanford and Hanneman 1982) and Long et al. (2004) recorded vine vigor measurements in their methods but did not report the results. Over half of the N needed by the potatoes is taken up by the early bulking period, and excessive N applied late in the season can also decrease specific gravity and

skin set (Stark and Westermann 2008). Biemond and Vos (1992) state bulking rate is a function of leaf area index at tuber initiation, and that the timing and placement of N applications is more important for early cultivars than late cultivars (Maidl 1995). N response is also genotype specific (Kanzikwera et al. 2001), and will vary by variety.

P will impact early crop development and tuber initiation and tuber maturity; deficiency will decrease tuber yield, size, and specific gravity (Stark and Westermann 2008). Both P and K increase root growth and plant height. P impacts early season leaf area, while K increases leaf area at later growth stages (Reddy et al. 1986). Potatoes grown under high K produced lower aboveground biomass (Tawfik 2001). K application increases leaf P concentration, but N application decreases P concentration in the leaf (Kanzikwera et al. 2001). However, yield responses to these nutrients differ. Sharma and Arora (1987) observed that N and K application increased the number and yield of medium and large tubers. P application increased the yield of small and medium tubers while decreasing larger tuber yield. The effect of farmyard manure followed the same trend as either inorganic N or K application. When both manure and fertilizer was applied, the potato response to inorganic N increased, and response to inorganic P and K decreased. Responses to inorganic P and K are weather dependent as well; cool seasons result in a greater P response, while a greater K response is evident in a more conducive growing season.

Much work has been conducted on K alone with respect to yield. K directly impacts yield, tuber size, and quality factors such as specific gravity, bruising, fry color, and storability. Deficiencies will decrease dry matter and starch formation, and excess K will reduce specific gravity by increasing tuber water content (Laboski and Kelling 2007; McDole et al. 1978; Westermann et al. 1994). The optimum tuber K level is 1.8% for maximum dry matter production (Stark and Westermann 2008). K application increases large and medium tuber yield

and decreases small tuber yield (Grewal and Trehan 1993; Kanzikwera et al. 2001; Sharma and Arora 1987; Tawfik 2001). However, at high levels of K application, the total yield may decrease (Guenther and Schotzko 2008; Panique et al. 1997). Grewal and Trehan (1993) also suggest that K application increases water use efficiency with regard to tuber yield per mm water, especially in rain-fed crops under drought conditions during plant emergence and tuber initiation. Response to K is more pronounced in rapid-bulking varieties with large tubers than in longer-duration varieties producing a large proportion of small tubers.

S is an important part of many enzymes and defense compounds like glutathione, and S application may be important in soils with low S levels. Deficiency of Ca, an essential nutrient for cell wall and membrane stability (Epstein and Bloom 2005; Havlin et al. 2005), may cause internal defects like brown spot and brown center. Mg is an essential component of chlorophyll molecules in plants (Epstein and Bloom 2005), and elevated K concentrations in soil with low Mg levels (high K:Mg ratios) can cause Mg deficiency (Guenther and Schotzko 2008).

Like Ca, B is important for cell wall stability but dicotyledonous plants typically contain more B than grasses (Epstein and Bloom 2005; Havlin et al. 2005). Both B and Zn are involved in hormone regulation of indole acetic acid and auxin accumulation (Havlin et al. 2005; Puzina 2004), enzyme activity, and protein synthesis (Epstein and Bloom 2005; Shashidhar 2006). Low Fe levels in the roots may decrease activity of peroxidases, which are important enzymes involved in plant defense (Shashidhar 2006). Fe deficiency can also impact chlorophyll content and production (Amberger 1974) and ATP synthesis (Epstein and Bloom 2005). Copper (Cu) is an important enzyme component involved in carbon and nitrogen metabolism during the vegetative stage (Shashidhar 2006), and can affect lipid structure in cell membranes (Havlin et

al. 2005). Mn is also an important component of enzymes involved in plant defense, the citric acid cycle (Shashidhar 2006), and lignin production (Havlin et al. 2005).

Nutrient uptake by potatoes has been examined by multiple researchers. ‘Russet Burbank,’ a determinate late-maturing russet variety (PAA 2009), has been shown to accumulate around 260 kg K, 200 kg N, 27 kg P, and 22 kg S per hectare in a season (Stark and Westermann 2008), however daily accumulation rates varies by growth stage. Uptake of K during tuber initiation through mid-bulking is 4 kg ha^{-1} , but slows to 1.5 kg ha^{-1} during late bulking. N uptake averages 2.25 kg ha^{-1} from tuber initiation to maturation. P uptake is much lower, ranging from $0.25\text{-}0.70 \text{ kg ha}^{-1}$ during tuber bulking, with S uptake following a similar trend. Gunasena (1969) states potatoes utilize 2.28-3.57 kg N, 0.04-0.12 kg P, and 3.7-5.41 kg K per tonne of fresh tuber weight. Sufficient micronutrient levels (mg kg^{-1}) in entire leaf samples during tuber bulking are: >20 of Zn, >30 of Fe, >5 of Cu, and >20 of Mn. In Indian cultivars, micronutrient responses appear to be cultivar specific (Trehan and Sharma 1999). These researchers also examined micronutrient content of tubers for 19 cultivars, and observed concentrations of $10\text{-}18 \text{ mg kg}^{-1}$ Zn, $21\text{-}53 \text{ mg kg}^{-1}$ Fe, $2.0\text{-}4.3 \text{ mg kg}^{-1}$ Cu, and $5\text{-}31 \text{ mg kg}^{-1}$ Mn (Trehan and Sharma 1996).

Soil nutrient availability is affected by multiple factors (Stark and Westermann 2008). Soil pH influences nutrient availability, with most nutrients available from pH 6.5 to 7.0. Ca, Mg, P, and molybdenum (Mo) deficiency symptoms as well as Mn, aluminum (Al), and ammonium (NH_4^+) toxicity symptoms appear at pH below 5.0. However, at pH above 5.2 common scab (*Streptomyces scabies*) incidence can increase (Pavlista 2008). At pH above 7.5,

B, Fe, Zn, Mn, and Cu deficiencies appear. P may precipitate as calcium phosphate in calcareous soils as well. Nutrient availability is also impacted by water conditions. Most nutrients enter the roots through mass flow or diffusion, which both require nutrients to be dissolved in water (Foth 1990). Soil temperature can affect plant growth and N availability through its effect on the rate of organic matter mineralization by microbes. Soil organic matter can be a slow-release and stable nutrient source by increasing micronutrient availability and chelating metal ions. Plants grown in amended soils rarely experience micronutrient deficiencies (Stark and Westermann 2008).

Weeds. Three summer annual weeds that can impact potato production systems are hairy nightshade (*Solanum physalifolium* Rusby), giant foxtail (*Setaria faberi* Herrm.), and common lambsquarters (*Chenopodium album* L.). These weeds affect crop growth by competing with potatoes for water, space, light, and nutrients. Shantz and Piemeisel (1927) observed similar water use efficiency values of the C₃ weeds common lambsquarters and cutleaf nightshade (*Solanum triflorum* Nutt.) to that of C₃ potato (1.5-2.0 mg dry weight g⁻¹ water). The leaf water use efficiency of common lambsquarters and C₄ giant foxtail at 300 ppm CO₂ levels were 4.6 and 12.9 mg CO₂ g⁻¹ water, respectively (Carlson and Bazzaz 1982).

Limited research is available on weed nutrient content. Green foxtail [*Setaria viridis* (L.) P.Beauv.] nutrient concentration at pH 6.0 after corn silking was 3.49% N, 4.56% K, 0.30% P, 0.68% Ca, 0.65% Mg, and 0.26% S (Weaver and Hamill 1985), and micronutrient concentrations were 290 mg kg⁻¹ Mn and 260 mg kg⁻¹ Zn. Competition of green foxtail with corn (*Zea mays* L.), Powell amaranth (*Amaranthus powellii* S. Wats.), or velvetleaf (*Abutilon theophrasti*

Medic.) did not affect nutrient uptake. Liebman et al. (2004) observed that swine (*Sus scrofa*) compost increased P and K content in the stems of giant foxtail and common waterhemp (*Amaranthus rudis* Sauer), as well as N and K content in velvetleaf stems.

A greenhouse competition examined 'Atlantic' and Russet Burbank in competition with redroot pigweed (*Amaranthus retroflexus* L.) and barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.]. The competitive ability of potato was greater than redroot pigweed and equivalent to that of barnyardgrass (Vangessel and Renner 1990b). In another greenhouse study, Hutchinson et al. (2011) observed Russet Burbank was more competitive than hairy nightshade (*Solanum physalifolium* Rusby) regardless of weed emergence timing, but reported 'Russet Norkotah' was less competitive when hairy nightshade emerged prior to potato.

In the field Hutchinson et al. (2011) examined hairy nightshade in competition with the same two potato varieties, and observed yield reductions in Russet Burbank from as few as two hairy nightshade plants per meter of row. Even though a significant yield reduction was not observed in Russet Norkotah, the hairy nightshade plants produced 3 times as much biomass and 6 times more berries than plants grown in competition with Russet Burbank. In the field component of Vangessel and Renner (1990b), four redroot pigweed or barnyardgrass plants per meter of row decreased Atlantic yield by 40% when planted within rows. When the same weed species were planted between the rows following hilling at the same density, no yield reduction was observed. A second experiment by Vangessel and Renner (1990a) allowed natural populations to emerge in the fields. Weed presence decreased yield of Atlantic and Russet Burbank variety potatoes, but early hilling decreased weed pressure and increased yield in one year suggesting an early hill may be beneficial for weed control. If weeds were removed after 20-cm potato height, competition with summer annuals at 1 to 5 plants m⁻² (mainly common

lambsquarters) reduced yield of 'Mirta,' a yellow flesh variety (Ciuberkis et al. 2007). When cultivation for weed control was timed at 60% predicted weed emergence, the greatest yield was observed (Felix et al. 2009). A mixed weed population of grass and broadleaf weeds emerging 2-25 days after potato emergence also reduced potato yield and tuber size, and green and yellow foxtail [*Setaria pumila* (Poir.) Roem. & Schult.] at 77 plants m⁻² reduced yield by 25% (Nelson and Thoreson 1981).

Weed seed production, viability, and dormancy may be affected by maternal influences of the weeds. As suggested by multiple researchers, environmental conditions in which the mother plant was grown may influence seed dormancy and survival (e.g., Kegode and Pearce 1998; Kigel et al. 1977; Naylor 1983). For example, Schutte et al. (2008) observed a maternal environment influence on velvetleaf and giant foxtail persistence in the soil. Lower seed dormancy can occur when maternal plants are grown under high temperatures, drought conditions, and high nitrogen (Fenner 1991). The maternal environment may be responsible for alterations in weed seed coat composition. The weed seed coat is maternally derived (Bewley and Black 1994) and is responsible for seed defense through physical and chemical mechanisms such as phenolic compounds, lignin, and complex carbohydrates (Kremer et al. 1984; Mohamed-Yasseen et al. 1994; Mullin and Xu 2001). Davis et al. (2008) reported differences in seed coat phenolic compound content in multiple weed species, and Schroeder et al. (1974) observed marked differences in seed fiber content. Weed seed survival may also be influenced by the environment in which the seed is buried (Fenner and Thompson 2005), particularly by affecting soil moisture during the burial period (Schutte et al. 2008).

Compost Benefits. Compost can be used as a nutrient source on farms to reduce livestock manure waste and fertilizer purchases (Menalled et al. 2005a). There are also benefits to using compost as a soil amendment, such as increasing soil organic matter, water and nutrient holding capacity, soil aggregation, and soil microbial activity (Gonzales and Cooperband 2002; Magdoff and van Es 2000; Salem et al. 2010). The composting process can kill plant pests like potato cyst nematode (Bøen et al. 2006), and compost amendments may also suppress disease (Entry et al. 2005) and increase arbuscular mycorrhizal spore populations (Douds et al. 1997). Compost has fewer viable weed seeds than fresh manure (Wiese et al. 1998), which may be beneficial with regards to weed management.

Compost in Potatoes and Weeds. There is limited research on compost effect in potatoes, but most studies observed an increase in yield after compost application. In a study conducted by LaMondia et al. (1999) on ‘Superior,’ a round white variety, 15 t ha⁻¹ spent mushroom compost (*Equus caballus*) increased the marketable tuber yield when compared to non-amended plots by 38-96%. However, 15 Mt ha⁻¹ spent mushroom compost may not increase yields in fumigated soils (Gent et al. 1998). These previous studies accounted amendment nutrient contributions by balancing N and K fertility with supplemental inorganic fertilizer. Adding 30 t ha⁻¹ of composted agro-industrial waste (a combination of olive husks, poultry manure, and confectionery wastewater) increased yield by 10% when compared to 30 t ha⁻¹ poultry manure (Rigane and Medhioub 2011). The agro-industrial waste compost contained less N and more K than the manure. Salem et al. (2010) examined compost addition (0, 40, 80, and 120 t ha⁻¹) to ‘Jelly’ potatoes, a yellow-fleshed variety, and observed an increase in marketable yield and

number as well as an increase in specific gravity, but this data was only reported for one growing season. Kleinhenz and Cardina (2003) observed a 13-14% marketable yield increase in three varieties of red-skinned potatoes grown under 6.5 t ha^{-1} dairy (*Bos taurus*) manure compost. Porter et al. (1999) observed Superior potato yield increased by 8 to 28%, and specific gravity decreased when amended with 22 t ha^{-1} waste potato compost plus 45 t ha^{-1} cattle manure, but failed to account for nutrient contributions from the amendments. Additionally, bulk density was not changed in the year of application, but bulk density decreased after three annual applications. Gallandt et al. (1998) observed four and five consecutive years of 22 t ha^{-1} cull potato compost plus 45 t ha^{-1} beef cattle manure (supplemented with inorganic fertilizer additions each year) resulted in equivalent yields to potatoes grown without amendments under weed free conditions.

The effect of compost on weeds has also been investigated. Amisi and Doohan (2010) observed increasing rates of composted dairy manure (0, 18, 36, and 54 t ha^{-1}) can decrease redroot pigweed emergence and can increase seed production. Menalled et al. (2005a) also observed a delay in emergence of giant foxtail and common waterhemp when composted swine manure was applied at all rates (8, 16, 24 Mg C ha^{-1}) for common waterhemp and at the 16 and 24 t C ha^{-1} rates for giant foxtail. However, composted swine manure applied at lower rates (4 or 8 t C ha^{-1}) did not impact weed seed survival, longevity, or emergence of giant foxtail, common lambsquarters, and common waterhemp (Menalled et al. 2005b). Applications of composted vegetable, fruit, and garden waste of 22.5 t ha^{-1} annually or 45 t ha^{-1} applied tri-

yearly reduced the seed-bank density of common lambsquarters and black nightshade (*Solanum nigrum* L.) (De Cauwer et al. 2009).

Blackshaw et al. (2005) observed composted cattle manure at 30 t ha⁻¹ did not increase downy brome (*Bromus tectorum* L.), field pennycress (*Thlaspi arvense* L.), and flaxweed [*Descurainia sophia* (L.) Webb ex Prantl] biomass, percent shoot N, or seed-bank numbers when compared to broadcasted conventional fertilizer in most cases. Similarly, spring application of 45 t ha⁻¹ beef manure and 22 t ha⁻¹ cull potato compost did not increase the biomass of common lambsquarters (*Chenopodium album* L.) in the first three years of application (Gallandt et al. 1998). When herbicides were used to control weeds, amending the soils did not affect the weed seed-bank numbers, but reduced seed-bank numbers when tillage alone was used to control weeds. Swine manure compost (8 t C ha⁻¹) did not increase giant foxtail and velvetleaf biomass, but did increase biomass of common waterhemp and seed production of velvetleaf and common waterhemp (Liebman et al. 2004). Menalled et al. (2004) applied composted swine manure (4 or 8 t C ha⁻¹) and increased stem diameter and biomass of common waterhemp, but not soybean [*Glycine max* (L.) Merr.] yield. This could be attributed to the plant relative growth rate, which is negatively related to seed size (Seibert and Pearce 1993) and small-seeded species may be able to compensate for their lack of initial resources through rapid growth and nutrient uptake.

Mycorrhizae. Arbuscular mycorrhizal fungi (AMF) can impact soil conservation and soil and plant nutrition (Bethlenfalvay 1992), and can associate with an estimated 90% of plant species (Smith and Smith 2012). Brundrett et al. (1996) describes the AMF hyphae as mostly aseptate, multinucleate, can be double-walled, coiled or uncoiled, and form h-branches. Aseptate hyphae

will be present when similar strains of the same species fuse, but septate hyphae may be present if geographically separate hyphae fuse (Smith and Read 2008). In roots, hyphae are not located in the vascular bundles, and the vesicles that form between cortical cells may have multilayer walls (Brundrett et al. 1996).

Glomus spp. mycorrhizae, which can colonize many plant species, can be both *Arum*-type and *Paris*-type colonizers (Smith and Smith 2012). Colonization is more rapid with the *Arum*-type, which form straight hyphae that grow longitudinal between cells, whereas *Paris*-type produce coiled intracellular hyphae (Brundrett et al. 1996). Colonization of a plant species can vary by cultivar, and percent root colonization is not an accurate predictor of the mycorrhizal benefits; the extent of the external mycelium may be more important in P uptake than actual colonization. Additionally, multiple tillage events that destroy mycorrhizal hyphal networks can limit the benefits from potential colonization (Miller 2000; Ryan and Graham 2002). AMF spores can germinate in the absence of roots, but will increase in root presence because of flavonoids or a sesquiterpene called ‘branching factor’ (Smith and Read 2008).

Inoculum level, soil P content, light, and changes in pH can affect the length or biomass of hyphae (Smith and Read 2008). As soil inoculum level increases, colonization also increases but as soil P increases, colonization decreases. Soil P can decrease growth tube development in spores, hyphal development, and may inhibit the branching factor signaling chemical or its production. Elevated soil P levels may also decrease the growth of hyphae in roots, possibly due to lower C availability. A plant response to inoculation with AMF at extractable P levels above 50 to 140 mg kg⁻¹ is unlikely to occur (Amijee et al. 1989; Thingstrup et al. 1998).

Mycorrhizal abundance and diversity of species can decrease in the presence of N (Johnson et al. 2003; Treseder 2004), and AMF facilitation of N uptake has been more variable.

While there has been evidence that AMF will transfer N to the plant, there is no difference in plant tissue N content. The N being transported to the plant is suspected to be inorganic in form (Smith and Read 2008). In addition, AMF can also increase plant uptake of Zn and Cu. AMF may also influence water relations; increases in plant growth may have been due to an increase in nutrient supply because of more water transport. Supplying soluble nutrients eliminated the AMF effect (Smith and Read 2008). To measure AMF colonization, many studies will sterilize soil with autoclaves; however, autoclaving can increase the available soil P and N content (Eno and Popenoe 1964; Ferriss 1984; Heinrich and Patrick 1986) and may reduce AMF colonization.

Many agriculturally significant weeds have also been shown to form AMF associations including black nightshade (*Solanum nigrum* L.) and giant foxtail (Jordan and Huerd 2008; Vatovec et al. 2005), while common lambsquarters is a non-host plant. In giant foxtail and black nightshade, Vatovec et al. (2005) conducted two greenhouse experiments harvested 42 days after planting; positive mycorrhizal effects were observed in one experiment and negative effects were observed of AMF in the second. Similarly, colonization of black nightshade and green foxtail reduced biomass production after 84 days in a greenhouse study (Veiga et al. 2011). Colonization of AMF was positively correlated to biomass production in 9 species, but the weeds examined are not typically problematic in potato cropping systems (Bilalis et al. 2011).

These fungi also colonize potato roots (Gerdemann 1968), which allows for increased nutrient uptake in exchange for photosynthates. Mycorrhizae have been shown to influence potato yield, but can be mycorrhizae species specific (Vosátka and Gryndler 2000). Douds et al. (2007) observed an increase in yield (33-45%) in Superior potatoes in one of two field experiments because of inoculum with AMF fungi, but colonization only ranged from 10-20%. In addition, shoot N concentrations were not affected and shoot P concentrations were not

affected in the study that had an increase in yield. When no yield increase was observed, there were differences in shoot P concentration, but the greatest concentration was observed in non-inoculated shoots. Atlantic potato minitubers experienced <1% colonization, but tuber yield was greater (48 to 85%) when grown in the presence of AMF inoculum (Niemira et al. 1995). Other studies in microplants and prenuclear minitubers have increased yield in the presence of AMF inoculum (Davies et al. 2005; Ryan et al. 2003). Variable yield responses have been observed when potatoes have been inoculated with a single isolate of AMF or an isolate mixture. Inoculation with *G. mosseae* alone did not increase yield in ‘Golden Wonder’ variety potatoes, but inoculation with *G. fasciculatum* did increase yield (Graham et al. 1976). Even within a species of AMF (*G. intraradices*), potato yield response varied by cultivar (Duffy and Cassells 2000; Niemira et al. 1995).

Herbicides, fungicides, and insecticides may affect AMF. Diuron did not influence mycorrhiza (Johnson and Pfleger 1992). Alachlor decreased root biomass at 2-4 kg ha⁻¹ but did not alter P levels, which indicates root damage rather than inhibition of colonization (Moorman 1994). Fertilizer application can negatively impact colonization when applied alone (P or K), but when applying balanced amounts of P, K, and N, the negative impact was reduced (Moorman 1994). Foliar fungicides, like chlorothalonil and mancozeb, may affect AMF colonization, but inhibition of the fungus has been shown to be minor (Simpson, personal communication, 2011).

Soil Enzymes and Seed Coat Degradation. Researchers have suggested soil carbon may influence the amount of microbial activity (Davis et al. 2005), and Davis et al. (2006) observed a negative correlation between organic matter addition and soil fungal 18sRNA values. However, Ullrich et al. (2011) observed no consistent relationship between microbial biomass and weed

seed decay, but did mention that measurements of specific microbial functions, such as soil enzyme activity, may reveal a link between microbial activity and seed decay. β -1,4-glucosidase (BG) is an enzyme involved in the degradation of cellulose in soil through hydrolysis of the disaccharide cellobiose into two separate glucose molecules (Muruganandam et al. 2009; Wernette 2011). β -1,4-*N*-acetyl glucosaminidase (NAG) is a type of enzyme that degrades chitin, and may degrade fungal pathogens (Tronsmo and Harman 1993). Both BG and NAG activity are thought to be positive soil health indicators (Muruganandam et al. 2009). Both phenol oxidase (PHENOX) and peroxidase (PEROX) can degrade lignin (Sinsabaugh 2010). PEROX will depolymerize lignin, while PHENOX will oxidize the phenolic components.

Soil enzyme activity may impact weed seed survivability by affecting the physical and chemical defense mechanisms of seeds. Phenolic compounds are produced by seeds as secondary defense mechanisms (e.g., Davis et al. 2008; Kremer 1993; Mohamed-Yasseen et al. 1994). In addition, seed survival is related to seed coat thickness and hardness (Davis et al. 2008; Kremer et al. 1984; Mullin and Xu 2001; Rodgers 1998). These parameters are influenced by cellulose, hemicellulose, and lignin content of the seed coat. As soil enzyme activity increases, degradation of secondary metabolites and seed coat may affect seed survival. Seeds may be more vulnerable to disease and predation, or may be more apt to germinate by reducing physical dormancy restrictions.

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CHAPTER 2

Cured Dairy Compost Influence on Weed Competition and Potato Yield

Introduction

Potato (*Solanum tuberosum* L.) is a perennial crop grown globally as an important food source. Production in the United States is over 36 million tonnes (35 t ha^{-1}) annually with a market value of over three billion dollars (USDA-NASS 2011). In irrigated production systems, growers utilize multiple tillage and irrigation events to maximize yield. However, intensive tillage and limited rotations may reduce the sustainability of potato cropping systems. Applying compost as a soil amendment builds soil carbon (C), increases water and nutrient holding capacity, and enhances soil microbial activity (Gonzales and Cooperband 2002; Magdoff and van Es 2000; Salem et al. 2010). Compost amendments may also suppress soil diseases (Entry et al. 2005) and increase arbuscular mycorrhizal spore populations (Douds et al. 1997). Both compost and manure can be used as nutrient sources to reduce fertilizer purchases (Menalled et al. 2005a), but compost contains fewer viable weed seeds as compared to fresh manure (Wiese et al. 1998).

There is limited research on the competitiveness of weeds in potato production systems. A mixed weed population of grass and broadleaf weeds emerging up to 25 days after potato emergence reduced potato yield and tuber size by 15 to 25% (Nelson and Thoreson 1981), but removal of weeds by 20-cm potato height minimized yield loss (Ciuberkis et al. 2007). In a field experiment by Vangessel and Renner (1990a), natural weed populations emerging in ‘Atlantic’ and ‘Russet Burbank’ cultivar potatoes reduced yield, but early hilling of the potatoes in one of two years decreased weed pressure and increased yield. In another study, timing cultivation and

herbicide application at 60% predicted weed emergence resulted in the greatest tuber yield (Felix et al. 2009). As few as one barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.] or redroot pigweed (*Amaranthus retroflexus* L.) plant per m of row decreased marketable tuber yield of Atlantic potatoes in Michigan by 19 and 33%, respectively (Vangessel and Renner 1990b). In other field research in Idaho, two hairy nightshade (*Solanum physalifolium* Rusby) plants per m row reduced Russet Burbank marketable yield by 10% while one plant per m row reduced marketable tuber yield of 'Russet Norkotah' by 21% (Hutchinson et al. 2011). Hairy nightshade plants had three times as much biomass and six times more berries when grown with Russet Norkotah as compared to plants grown in competition with Russet Burbank.

Atlantic and Russet Burbank potatoes were more competitive than redroot pigweed and equivalent in competitiveness to barnyardgrass (Vangessel and Renner 1990b). In another greenhouse study, Russet Burbank was more competitive than hairy nightshade regardless of weed emergence timing and Russet Norkotah was less competitive when hairy nightshade emerged prior to potato (Hutchinson et al. 2011).

The effect of compost on weed growth has been documented by numerous researchers. Blackshaw et al. (2005) observed no effect of fall or spring applied beef cattle (*Bos taurus*) compost (30 t ha⁻¹) on biomass accumulation of downy brome (*Bromus tectorum* L.), field pennycress (*Thlaspi arvense* L.), and flixweed [*Descurainia sophia* (L.) Webb ex Prantl] in wheat (*Triticum aestivum* L.). Similarly, spring application of 45 t ha⁻¹ beef manure and 22 t ha⁻¹ cull potato compost did not increase the biomass of common lambsquarters (*Chenopodium album* L.) in the first three years of application (Gallandt et al. 1998). Common lambsquarters emergence was not influenced by swine manure (*Sus scrofa*) compost (Menalled 2005b). Swine manure compost at 8000 kg C ha⁻¹ increased biomass and seed production of common waterhemp

(*Amaranthus rudis* Sauer), but did not increase velvetleaf (*Abutilon theophrasti* Medic.) and giant foxtail (*Setaria faberi* Herrm.) biomass (Liebman et al. 2004) or soybean [*Glycine max* (L.) Merr.] yield (Menalled et al. 2004). However, the effect of compost on hairy nightshade competition has not been examined.

There is limited research on how compost affects potatoes. In ‘Superior,’ a round white potato cultivar, 15 t ha⁻¹ spent mushroom compost (*Equus caballus*) increased the marketable tuber yield when compared to non-amended plots by 38 to 96% (LaMondia et al. 1999), but higher rates (15 Mt ha⁻¹) of the same material may not increase yields in fumigated soils (Gent et al. 1998). Porter et al. (1999) observed Superior potato yield increased by 8 to 28%, and specific gravity decreased when amended with 22 t ha⁻¹ waste potato compost plus 45 t ha⁻¹ cattle (*Bos taurus*) manure, but failed to account for fertility additions from the amendments. Gallandt et al. (1998) observed four and five consecutive years of 22 t ha⁻¹ cull potato compost plus 45 t ha⁻¹ beef cattle manure (supplemented with inorganic fertilizer additions each year) resulted in equivalent yields to potatoes grown without amendments under weed free conditions. Adding 30 t ha⁻¹ composted agro-industrial waste (a combination of olive husks, poultry manure, and confectionery wastewater) increased yield by 10% when compared to 30 t ha⁻¹ poultry manure alone (Rigane and Medhioub 2011). Salem et al. (2010) examined compost addition (0, 40, 80, and 120 t ha⁻¹) to ‘Jelly’ potatoes, a yellow-fleshed cultivar, and observed an increase in marketable yield and number as well as an increase in specific gravity. Kleinhenz and Cardina (2003) observed a 13 to 14% marketable yield increase in three cultivars of red-skinned potato from 6.5 t ha⁻¹ dairy (*Bos taurus*) manure compost. Potato response to N is cultivar specific

(Kanzikwera et al. 2001), and none of these studies were with the round white cultivar ‘Snowden’ (a common chipping cultivar in Michigan). There have also been no published reports of weed competition in potato as influenced by the addition of compost. Therefore, the objectives of this research were to investigate the impact of cured dairy manure compost on weed competition in potato and weed seed production, and evaluate the effect of compost and weed competition on potato growth and yield.

Materials and Methods

A field experiment was established in 2010 and repeated in 2011 at the Michigan State University Montcalm Research Center near Entrican, MI. This study was conducted in a two-way factorial randomized complete block design with four replications. The first factor was cured dairy manure compost rate at 0, 4000 or 8000 kg carbon (C) ha⁻¹, and the second factor was weed species with three species and a weed-free control. The species were common lambsquarters (CHEAL), giant foxtail (SETFA) or hairy nightshade (SOLSA). The soil was a mixture of Montcalm loamy sand and sandy loam (coarse-loamy, mixed, semiactive, frigid Alfic Haplorthods) and McBride loamy sand and sandy loam (coarse-loamy, mixed, semiactive, frigid Alfic Fragiorthods) with 1.1% organic matter and a pH of 6.9 in 2010 and pH of 6.7 in 2011 (Table 2.1). Each year the field was tilled in the fall with a chisel plow to a 30 cm depth or a disc to a 10 cm depth; spring tillage was a disc and/or a field cultivator to a 15 cm depth. The dates of tillage, fertilizer applications, cultivations, and harvests are in Table 2.2.

Compost Application. Composted dairy manure¹ that had been curing for 2 to 4 months was applied manually to 6.1 x 3.4 m plots and incorporated to 10 cm using a disc. A complete soil

Table 2.1. Initial soil test and cured dairy manure compost nutrient measurements.^a

Soil Property	2010		2011	
	Soil	Compost	Soil	Compost
pH	6.9	9.3	6.7	8.6
Organic Matter (%)	1.1	55.7	1.1	49.5
Carbon Content (%)	-	32.3	-	28.7
Water Holding Capacity (%)	-	-	5.28	15.0
Cation Exchange Capacity [cmol(+)/kg]	3.6	-	3.0	-
	mg kg ⁻¹			
Total Nitrogen (N)	400	22600	450	20000
Inorganic N (Ammonium-N/Nitrate-N)	-	-	3.1/3.1	27/381
Phosphorus	200	5200	224	7200
Potassium	182	19300	142	23100
Magnesium	88	11300	77	16900
Calcium	483	43600	401	57700
Sulfur	12	3200	9	4600
Boron	-	26	0.1	37
Copper	4.3	71	3.0	102
Manganese	13.2	291	10.8	312
Zinc	2.0	137	1.5	212
Iron	31.7	3056	24.8	3195
Sodium	11	2800	5	5300
Aluminum	-	1295	-	794

^aSoil and compost measurements containing a dash were not measured.

and compost nutrient analysis was conducted in both years prior to compost application (Table 2.1). Potassium (K) fertilizer was applied to the non-amended plots at 47 kg K ha⁻¹ (0N-0P-17.4K, 21S, 10Mg²), and was not applied to composted plots because approximately 90% of the K in the compost was estimated to be released in-season (Rosen and Bierman 2005). Potatoes were planted (cut seed, approximately 42 to 47 g; Snowden cultivar) mid-May each year (Table 2.2) in 0.86 m rows with 27 cm seed spacing at a 10 cm depth. Nitrogen (N) was balanced based on expected total inorganic N application from the compost and inorganic fertilizer (LaMondia et al. 1999; Nyiraneza and Snapp 2007). A summary of total macronutrient applications in 2010 and 2011 is

Table 2.2. Schedule of various activities in the field.^{a,b}

Event	Time of Implementation	
	2010	2011
Fall tillage ^c	October 8, 2009	October 8, 2010
Spring tillage ^d	April 29	May 4
Compost and K fertilizer application	April 29	May 4
Weeds planted in greenhouse	May 7	May 12
Potato planting	May 17	May 20
Preemergence herbicide application	May 19	May 20
Potato cracking and weed transplant (0 DAC)	June 7	June 7
Potato cultivation and N application	June 15	June 15
14 DAC harvest	June 21	June 21
Potato hilling and N application	June 24	June 27
28 DAC harvest	July 6	July 5
Topdress N application at canopy closure	July 7	July 7
42 DAC harvest	July 19	July 19
56 DAC harvest	August 2	August 2
End-of-season weed harvest	September 9	September 6
Final weed control application	September 10	September 7
Potato harvest	September 30	September 28

^a Abbreviations: K, potassium; DAC, days after cracking; N, nitrogen.

^b Soil and compost measurements containing a dash were not measured.

^c Fall tillage consisted of using a disc in 2009 and a chisel plow in 2010.

^d Spring tillage consisted of using a disc in 2010 and using a disc followed by a field cultivator in 2011.

Table 2.3. Macronutrient application total in 2010 and 2011 by compost rate.^a

Nutrient	0 kg C ha ⁻¹		4000 kg C ha ⁻¹		8000 kg C ha ⁻¹	
	<u>2010</u>	<u>2011</u>	<u>2010</u>	<u>2011</u>	<u>2010</u>	<u>2011</u>
	mg kg ⁻¹					
Inorganic-N	116	121	116	118	115	115
P	4	4	27	34	50	64
K	17	17	103	114	206	228
Ca	0	0	258	317	517	635
Mg	5	5	67	93	134	186
S	21	21	19	25	38	51

^a Abbreviations: C, carbon; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; S, sulfur.

given in Table 2.3. Starter fertilizer in the 0 kg C ha⁻¹ plots in 2010 was applied at 59.4 kg N ha⁻¹ (24.4N-2.9P-0K³) and at 67.4 kg N ha⁻¹ (24.8N-2.7P-0K⁴) in 2011. Starter fertilizer application was reduced in the composted plots in both years based on expected inorganic N release from the amendment. Because N mineralization from composted dairy manure solids has been shown to range between -5 and 20% (Gale et al. 2006; Hartz et al. 2000; Rosen and Bierman 2005), we estimated 10% of the total N content would mineralize in the first season.

Potatoes received additional applications of N at cultivation (66.7 kg N ha⁻¹ of 28N-0P-0K⁵) and hilling (41.0 kg N ha⁻¹ of 46N-0P-0K⁶), and prior to canopy closure (41.0 kg N ha⁻¹ of 46N-0P-0K). Natural weed populations were controlled after planting using 0.23 kg ai ha⁻¹ linuron⁷ + 0.58 kg ai ha⁻¹ S-metolachlor⁸ applied with a six-nozzle (50 cm spacing) carbon dioxide backpack sprayer at 190 L ha⁻¹ and 330 kPa with TeeJet® XR8003 nozzles⁹ 45 cm above the soil surface. Irrigation¹⁰ was applied as needed to supplement natural rainfall (Table 2.4). Rainfall and growing degree day accumulation (base 4°C) were recorded using the Michigan State University Enviro-weather station in Entrican, MI (Table 2.4). Fungicides¹¹⁻¹³ (Table 2.5) and insecticides¹⁴⁻¹⁷ were applied in-furrow or foliarly as needed to alleviate pest pressure using a two-nozzle (86 cm spacing) compressed air sprayer at 190 L ha⁻¹ and 240 kPa with XR8003 nozzles 45 cm above seed piece or a 16-nozzle (50 cm spacing) compressed air sprayer at the same volume and pressure, and with the same nozzle type 75 cm above the plant canopy.

Table 2.4. Growing degree day accumulation (base 4°C), and rainfall and irrigation summary by month.^a

Month	GDD	2010			GDD	2011		
		Rainfall	Irrigation	Total		Rainfall	Irrigation	Total
		cm				cm		
April	358.0	3.8	0.0	3.8	182.1	8.6	0.0	8.6
May	610.4	9.1	0.0	9.1	566.8	7.9	0.0	7.9
June	800.8	7.9	0.0	7.9	787.0	6.1	0.0	6.1
July	1013.1	3.6	10.4	14.0	1033.9	4.3	10.2	14.5
August	978.2	4.9	5.3	10.2	882.4	6.6	2.8	9.4
September	576.7	4.6	0.0	4.6	578.0	6.1	0.0	6.1
Total	4337.2	33.9	15.7	49.6	4030.2	39.6	13.0	52.6

^a Abbreviations: GDD, growing degree days.

Table 2.5. Insecticide and fungicide applications.

Product	2010			2011		
	Rate	Number ^{a,b}	Method	Rate	Number ^{c,d,e}	Method
	kg ai ha ⁻¹			kg ai ha ⁻¹		
chlorothalonil ¹¹	1.34	1,3,4,7	Foliar	1.34	1,2,3,4,5,6,7,8	Foliar
famoxadone + cymoxanil ¹²	0.084 + 0.084	-	Foliar	0.084 + 0.084	5,10	Foliar
	0.112 + 0.112	2,5	Foliar	0.112 + 0.112	6	Foliar
mancozeb ¹³	1.34	6,9,10,11	Foliar	1.34	9,10,11	Foliar
	1.24	8	Foliar			
	1.17	12	Foliar			
Insecticide						
	g ai ha ⁻¹			g ai ha ⁻¹		
imidacloprid ¹⁴	257	1	In-furrow	257	1	In-furrow
spinetoram ¹⁵	55.8	2	Foliar	-	-	-
dimethoate ¹⁶	83.7	3	Foliar	-	-	-
abamectin ¹⁷	-	-	-	12.6	2	Foliar

^a Numbers correspond to fungicide applications on the following dates: 1, 6/17; 2, 6/24; 3, 6/30; 4, 7/9; 5, 7/14; 6, 7/21; 7, 7/30; 8, 8/6; 9, 8/13; 10, 8/21; 11, 8/27; 12, 9/5.

^b Numbers correspond to insecticide applications on the following dates: 1, 5/17; 2, 6/30; 3, 7/9.

^c Numbers correspond to fungicide applications on the following dates: 1, 6/18; 2, 6/25; 3, 6/30; 4, 7/8; 5, 7/14; 6, 7/20; 7, 7/30; 8, 8/6; 9, 8/12; 10, 8/19; 11, 8/26.

^d Numbers correspond to fungicide applications on the following dates: 1, 5/20; 2, 7/20.

^e Applications 5, 6, and 10 contained multiple active ingredients in the same spray mixture.

Weed Establishment. Seed of common lambsquarters¹⁸, giant foxtail¹⁹, and hairy nightshade²⁰ were collected from the field and stored at 4°C. Prior to planting, weed seeds were stored at 22°C for 24 hr, and hairy nightshade seeds were submersed in 2 g L⁻¹ gibberellic acid to stimulate germination (Spicer and Dionne 1961; Edmonds 1986). Four to 10 seeds of each species were planted into 25 x 40 mm media plugs²¹ in the greenhouse at Michigan State University in East Lansing, MI 4 wk prior to transplanting at the field site. Plugs were thinned weekly to maintain a density of one plant per plug. Natural light was supplemented with artificial light for 16 hr per day at 400 µmol m⁻² s⁻¹ photosynthetic photon flux. Conditions in the greenhouse were maintained at day/night temperatures of 27/24°C.

A single species was transplanted into the second and third row of each plot (with the exception of the weed-free plots) at potato cracking (Table 2.2). Common lambsquarters and hairy nightshade were 2.5 cm tall at the time of transplanting, and giant foxtail was 7.5 cm tall. Weeds were transplanted into the row at a density of 5.3 plants m⁻¹ row to simulate weed emergence that would not be affected by cultivation and hilling. Transplants were watered after planting (3.80 L row⁻¹), and experienced a rainfall event of 0.25-0.5 cm within 48 hr of planting. Weed survival was evaluated one week after transplanting and weeds were thinned as needed to maintain plant density.

In-Season Measurements. Growth of the weeds and potatoes was measured at 14, 28, 42, and 56 days after cracking (DAC). Plant heights were measured, and plants were destructively harvested from the third row for fresh biomass measurements. Roots were separated and washed

for mycorrhizal colonization measurements. Above-ground material was oven-dried for 4 d at 60°C and weighed. Potato vine biomass was calculated by dividing biomass by the number of stems harvested. Additionally in 2011, soil moisture measurements²² to 12 cm depth and soil samples (15 cm depth, six per plot) were taken bi-weekly from the weed-free plots to monitor volumetric water content and inorganic N content. End-of-season measurements of above-ground material occurred at 94 DAC in 2010 and at 91 DAC in 2011. Soil samples were collected to 15 cm depth and analyzed for pH, N, P, K, Ca, Mg, S, and micronutrients. To control remaining weeds after potato senescence in 2010, 0.37 kg ai ha⁻¹ glufosinate²³ was applied using the 16-nozzle compressed air sprayer (190 L ha⁻¹, 240 kPa, TeeJet® XR8003 nozzles) 50 cm above the potato canopy. In 2011 plots were mowed to 15 cm height for weed control after potato senescence.

Weed Seed Production. Weeds were harvested at the end-of-season, oven-dried at 60°C for 7 d, and seeds mechanically separated from the plants. A 40-mL subsample of hairy nightshade berries from one plant per plot was separated into diameter classes (DC) and counted, and mature seeds were counted from 10 berries and averaged to obtain number of mature seeds per berry (*spb*) in each DC. In each DC, the berry count was divided by the weight to calculate the number of berries per gram (*bpg*). Next, the weight of each DC in the subsample was divided by the total subsample weight to obtain a percentage. The entire sample from each plant was weighed, and multiplied by the DC percentages of the subsample. The weight of each DC in the total sample was multiplied by *bpg* and *spb* to calculate total mature seed production per DC. All seed values from each DC were added together to obtain total mature seeds per plant.

Mature seed per plant was divided by the above-ground dry biomass to calculate mature seed production per gram dry biomass.

Common lambsquarters and giant foxtail seeds were sieved and passed through an air-column separator to remove excess chaff and immature seeds. A 0.5-g subsample of common lambsquarters and giant foxtail seed from each plot was counted and weighed; total sample weight was multiplied by seeds per gram to calculate mature seed production per plant, and divided by dry above-ground biomass to calculate mature seed per gram dry biomass.

Potato Tuber Yield and Quality Evaluation. Potatoes were mechanically harvested at the end of September each year. Tubers were graded by diameter into undersized tubers (<4.75 cm), marketable tubers (4.75-8.25 cm), and oversized tubers (>8.25 cm); tubers with growth aberrations or cracks were classed as cull tubers. Potatoes in each class were collectively weighed and counted. Marketable and oversized tubers were evaluated for internal defects of vascular discoloration, bacterial canker, and hollow heart. Common scab (*Streptomyces scabies*) severity was not rated because most tubers exhibited similar scab levels. Specific gravity of marketable tubers was measured using the weight in water-weight in air method (Westermann et al. 1994).

Mycorrhizal Analysis. After each harvest, roots were washed, cut into 1-cm segments, and preserved in 50% ethanol (Grace and Stribley 1991). Roots were cleared in 10% potassium hydroxide and stained with aniline blue following the procedure described by Grace and Stribley (1991). Five root segments of a root sample were wet mounted onto a microscope slide, and two slides were prepared per root sample. Slides were scanned under 200x magnification using a

transmitting light microscope and hyphae, arbuscules, and vesicles were counted using the magnified colonization intersections method (McGonigle et al. 1990) to estimate root colonization by arbuscular mycorrhizae.

Statistical Analysis. Data were analyzed using a one-way ANOVA with the MIXED procedure in SAS 9.2²⁴. Year, compost rate, weed species, and their interactions were treated as fixed factors, with replication as a random factor. Normality of the residuals was evaluated by visual examination of normal probability and stem-and-leaf plots. Homogeneity of the variances was evaluated by residual plots, box plots, and Levene's test ($\alpha=0.1$) and grouped to reduce the AIC value of the model using the GROUP option of the REPEATED statement. When the year by factor interaction was not significant, data were combined across years. When the interaction between compost rate and weed species was found to be significant, comparisons between the combinations at each compost application rate and weed species level were examined by slicing and conducting individual pair-wise comparisons using t-tests ($\alpha=0.05$). When factors were found to be significant ($P\leq 0.1$), all-pairwise comparisons were conducted using Fisher's protected LSD.

Results and Discussion

The compost rates used in this study may be in excess of what growers in Michigan would utilize. We applied 4 and 8 t C ha⁻¹, which was equivalent to a total compost application of 26 and 52 wet t ha⁻¹, respectively. These application rates are 10 to 15 times greater than

what an average producer would utilize in a single season (Otto, personal communication). These rates were used to attempt to emphasize differences because of compost application.

Effect of Compost on Weeds. Weed height (data not presented) and fresh above-ground biomass (Figure 2.1 a-e) were not affected by compost application 14, 28, 42, or 56 DAC ($P \leq 0.1$). Across compost application rates, common lambsquarters produced the greatest above-ground biomass, followed by hairy nightshade, and lastly giant foxtail. Gallandt et al. (1998) also observed no effect of spring applied beef cattle manure (45 t ha^{-1}) and cull tuber compost (22 t ha^{-1}) on biomass accumulation of common lambsquarters in the first year, and 8 t C ha^{-1} swine manure compost had no effect on giant foxtail and velvetleaf biomass in soybean (Liebman et al. 2004). Compost rate increased fresh above-ground biomass only within hairy nightshade at the end-of-season timing (Figure 2.1e). Year was significant at the 28 DAC timing because giant foxtail accumulated less biomass in 2011 compared to 2010.

Mycorrhizal colonization was $<3\%$ in potato and the weed species (data not presented). High soil phosphorus (P) levels ($>200 \text{ mg kg}^{-1}$ soil) may have limited colonization, as a response to mycorrhizae is unlikely at P levels above 50 to 140 mg kg^{-1} (Amijee et al. 1989; Thingstrup et al. 1998). Furthermore, percent colonization may not accurately predict mycorrhizal effects (Brundrett et al. 1996), and multiple tillage events, such as those utilized in potato production, that destroy mycorrhizal hyphal networks can limit the benefits from potential colonization (Miller 2000; Ryan and Graham 2002).

Compost did not influence weed seed production as measured by seed per plant or seed produced per gram of dry biomass (Table 2.6). Common lambsquarters produced the most seed

Figure 2.1. Weed and potato fresh above-ground biomass accumulation at (a) 14, (b) 28, (c) 42, (d) 56 days after cracking (DAC) and (e) at the end-of season at each compost rate. Uppercase letters are averaged across years, and lowercase are for 2010 and 2011, respectively. Letters of a to d denote differences between the species of common lambsquarters (CHEAL), giant foxtail (SETFA), hairy nightshade (SOLSA), and potato. Letters of v to z denote a significant species by compost rate interaction across years. Bars on the graph depict one standard error of the mean.

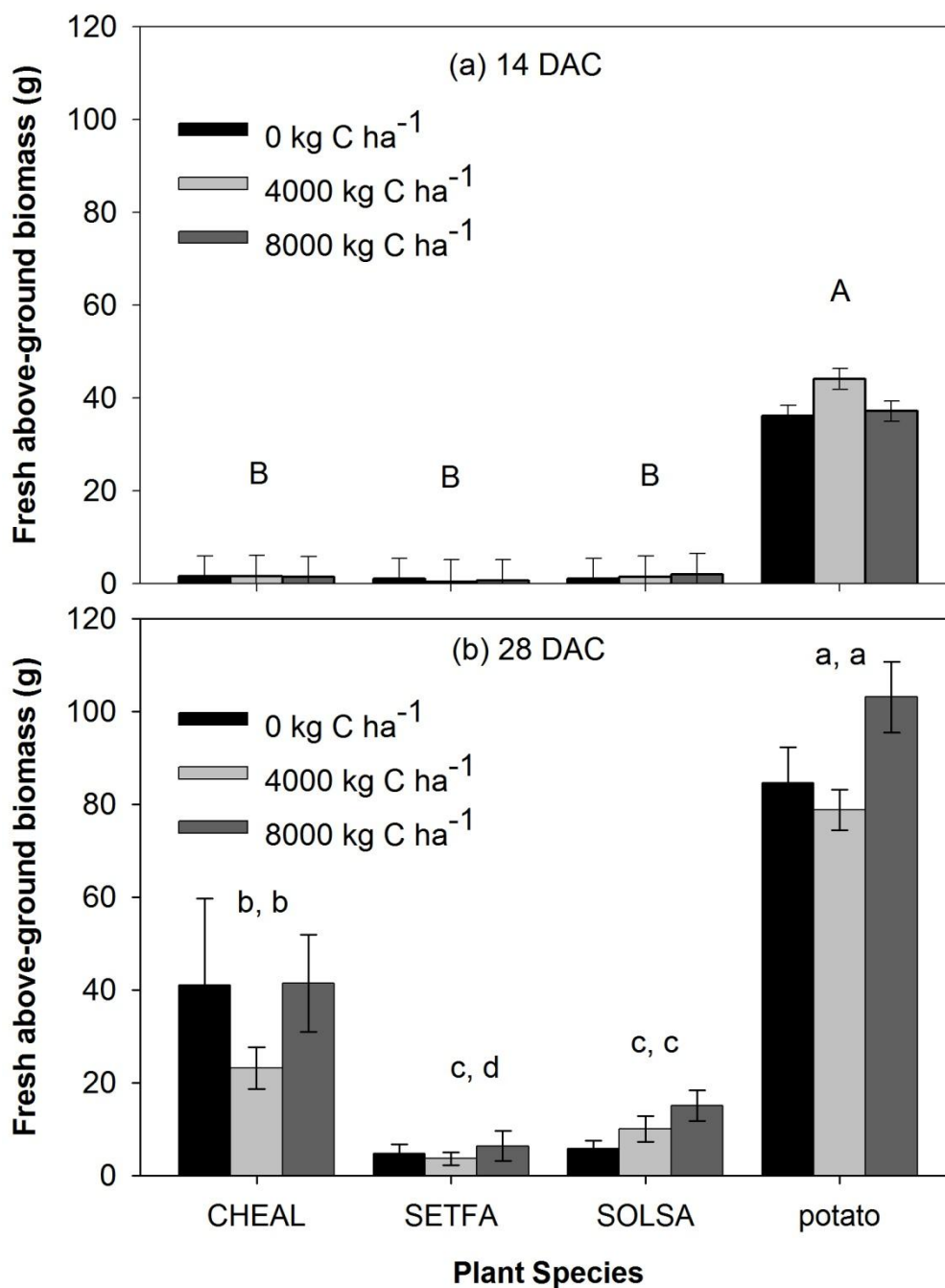


Figure 2.1 (cont'd).

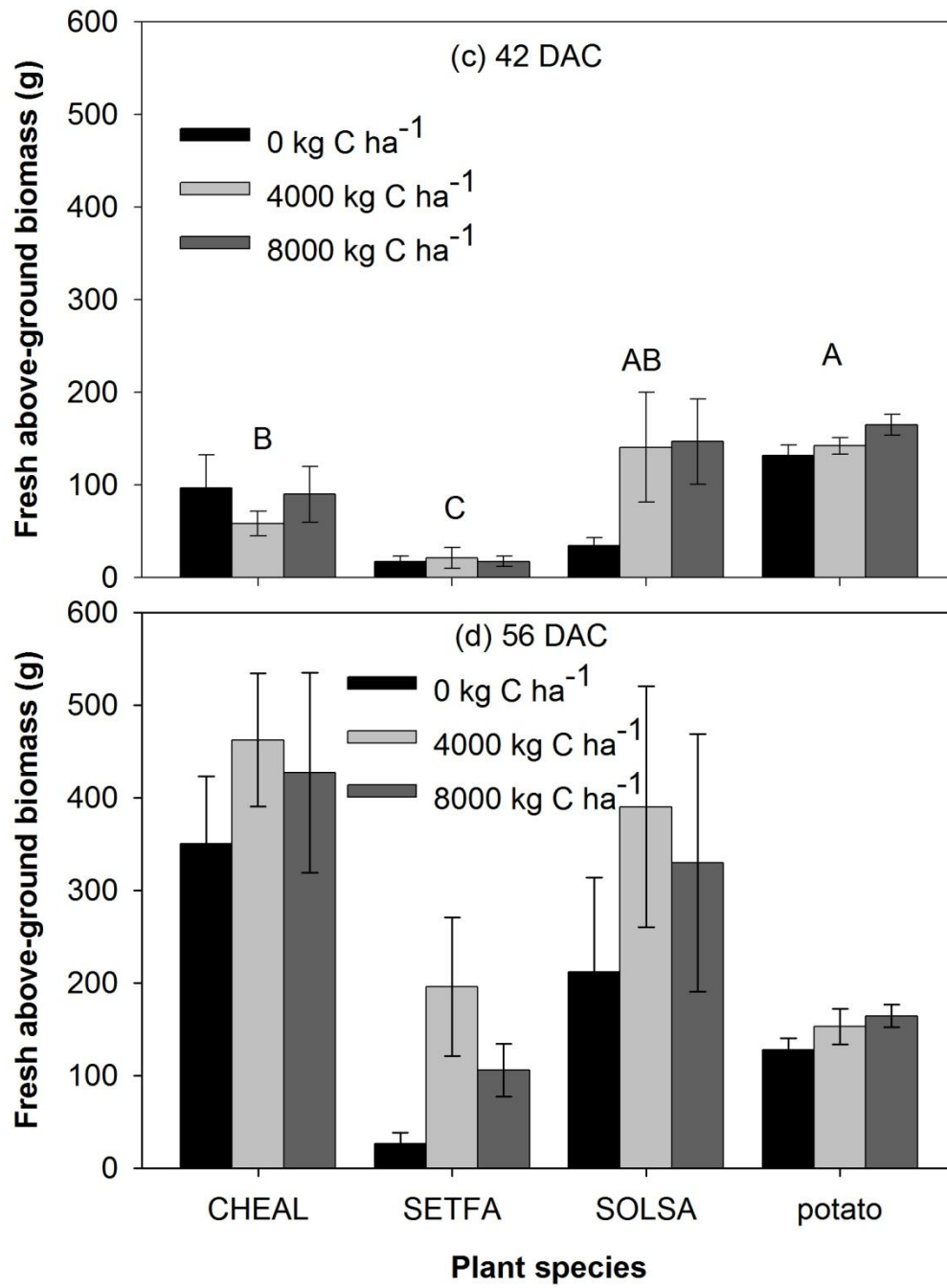


Figure 2.1 (cont'd).

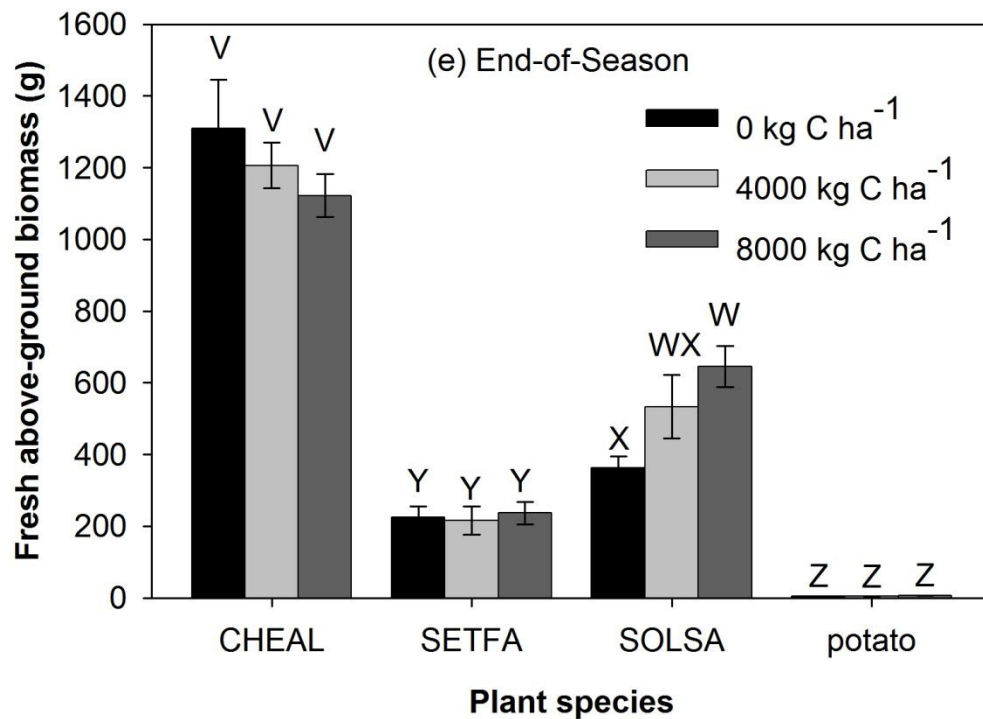


Table 2.6. Weed seed production as influenced by cured dairy manure compost application.^a

Species	Mature seeds plant ⁻¹				Mature seeds g ⁻¹ dry biomass			
	Compost rate (kg C ha ⁻¹)			LSD ^b (0.05)	Compost rate (kg C ha ⁻¹)			LSD (0.05)
	0	4000	8000		0	4000	8000	
CHEAL	111482	88788	89647	38870	247	226	258	71
SETFA	6159	6367	6100	4269	74	78	63	26
SOLSA	10284	13951	11696	7537	153	135	118	44

^a Abbreviations: C, carbon; LSD, least significant difference; CHEAL, common lambsquarters; SETFA, giant foxtail; SOLSA, hairy nightshade.

^b Means within a row greater than the LSD value are different from each other.

per plant, and giant foxtail produced the least seed per plant, averaged across compost treatments. In previous research, dairy manure compost increased redroot pigweed seed production (Amisi and Doohan 2010), and swine manure compost increased velvetleaf and common waterhemp seed production but had no effect on giant foxtail seed fecundity (Liebman et al. 2004).

Effect of Weeds on Potatoes. Weed competition did not influence potato height, but fresh vine biomass accumulation was typically greater in the weed-free compared to the weedy treatments ($P \leq 0.1$) at 14, 28, and 42 DAC (Figure 2.2 a-d). Differences in early season biomass may have

Figure 2.2. Potato vine biomass as affected by common lambsquarters (CHEAL), giant foxtail (SETFA), or hairy nightshade (SOLSA) competition at (a) 14, (b) 28, (c) 42, and (d) 56 days after potato cracking (DAC). Letters denote differences between species. Bars on the graph depict one standard error of the mean. P-value is the species effect on potato vine biomass.

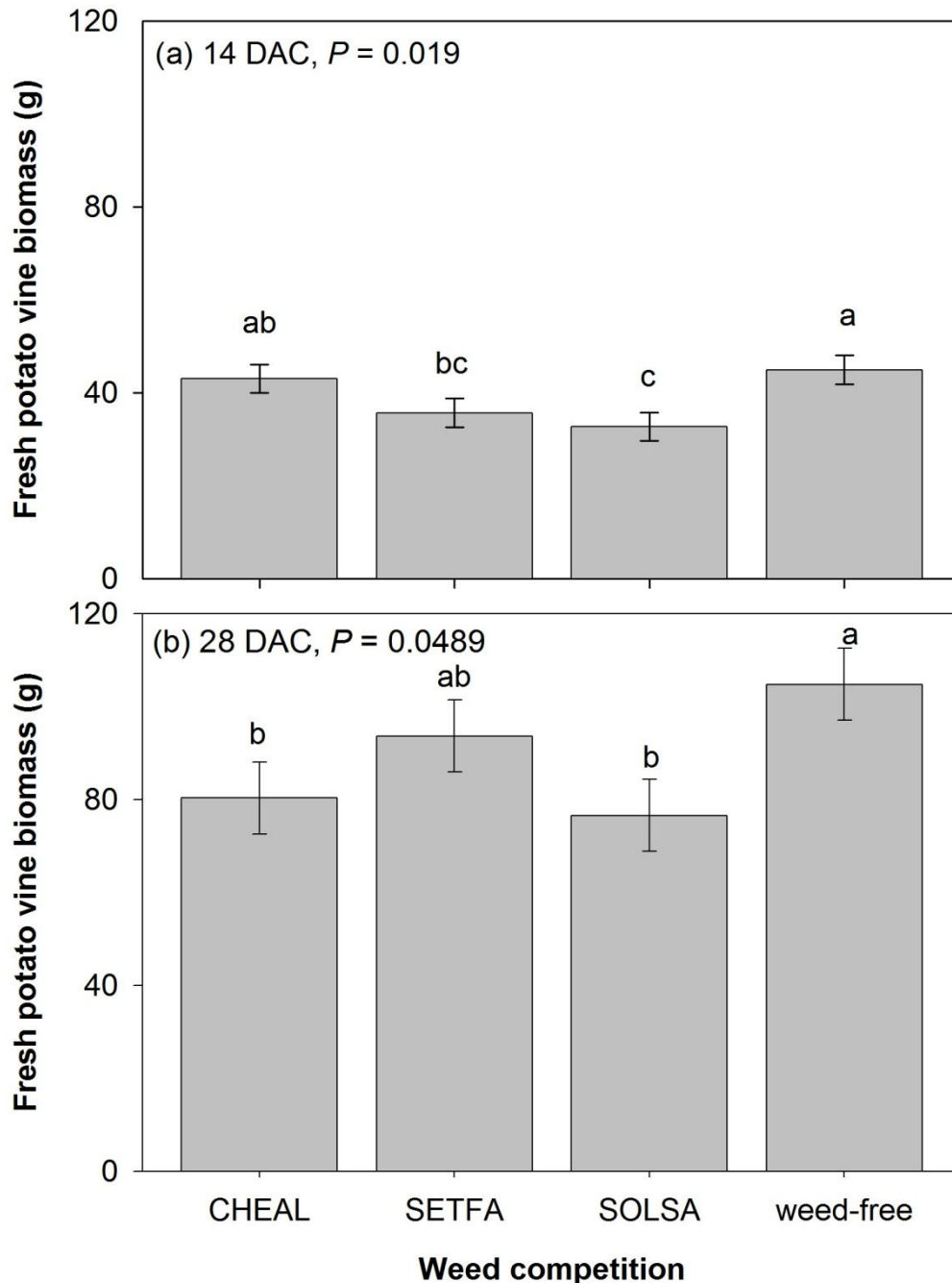
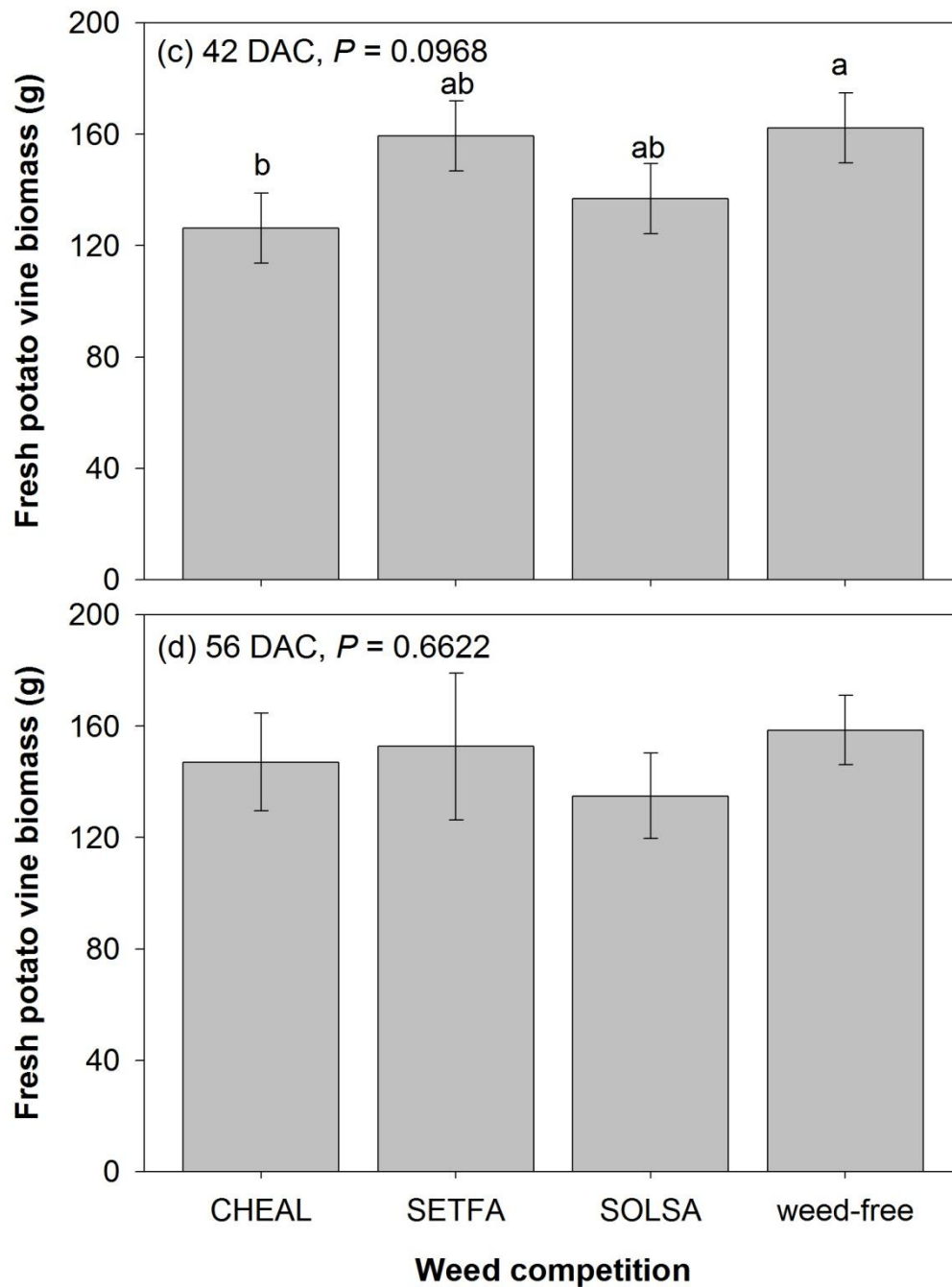


Figure 2.2 (cont'd).



contributed to tuber yield by allowing more photosynthate production during the early tuber bulking phase or resulting in a longer bulking phase, as the duration of bulking is critical to tuber biomass accumulation (Miller and Hopkins 2008). After the early bulking phase (42 DAC), weed biomass exceeded that of potato and the weeds began to shade the potatoes (Figure 2.1 d

and e). The growth of the weeds during the tuber bulking phase may have increased competition for light, and led to a reduction in potato yield.

Weed interference did not affect oversized tuber production, cull tuber production, or incidence of hollow heart, vascular discoloration, and bacterial canker (data not presented). The specific gravity of marketable tubers was also not influenced by weed competition (Table 2.7). Marketable tuber yield, marketable number, and total yield were greatest under weed-free conditions (Table 2.7). Five giant foxtail plants per m of row reduced marketable tuber yield, marketable number, and total yield by 17, 12, and 13%, respectively. Vangessel and Renner (1990b) observed a 40% decrease in marketable yield of Atlantic potatoes from four barnyardgrass or redroot pigweed m^{-1} planted within the row. Grassy weeds, mainly green foxtail (*Setaria viridis* L.) and yellow foxtail [*Setaria pumila* (Poir.) Roem. & Schult.], at 77 plants m^{-2} reduced tuber yield by 25% after season-long competition (Nelson and Thoreson 1981). Five hairy nightshade plants per m of row reduced marketable tuber yield, marketable

Table 2.7. Potato tuber yield and specific gravity as influenced by weeds or by compost rate.^{a,b}

Competition	SG	Tuber Yield			Tuber Number		
		Marketable	Undersize	Total	Marketable	Undersize	Total
		t ha^{-1}			$\times 10^3$ tubers ha^{-1}		
CHEAL	1.0757	14.6c	4.7	19.3c	149c	111b	260b
SETFA	1.0756	23.5b	5.5	29.1b	231b	129a	360a
SOLSA	1.0748	22.1b	5.7	28.0b	217b	133a	351a
weed-free	1.0754	28.4a	5.1	33.6a	262a	119ab	381a
Compost Rate							
(kg C ha^{-1})							
0	1.077A	20.7B	5.3	26.0B	205	124	329
4000	1.075B	22.1AB	5.2	27.3AB	214	121	335
8000	1.074B	23.6A	5.3	29.1A	226	124	350

^a Abbreviations: SG, specific gravity; CHEAL, common lambsquarters; SETFA, giant foxtail; SOLSA, hairy nightshade; C, carbon.

^b Lowercase letters denote significance within a column between weed species, and uppercase letters denote significance within a column between compost rates.

number, and total yield by 22, 17, and 17%, respectively (Table 2.7). Hutchinson et al. (2011) observed three hairy nightshade plants m^{-1} decreased marketable and total yield of Russet Burbank by 11 and 9%, respectively, while marketable and total yield of Russet Norkotah was reduced by 27 and 25%, respectively. This may indicate Snowden cultivar potatoes are more competitive with hairy nightshade than Russet Norkotah, but research needs to be conducted to compare the competitive ability of russets with round white potatoes in similar conditions to make this comparison. Giant foxtail and hairy nightshade did not significantly reduce total tuber number ($<10\%$), which indicates the yield reduction was primarily due to reduced tuber bulking. Competition at the time of tuber initiation may not have been great enough to limit tuber set, but competition during tuber bulking may have reduced tuber size.

Five common lambsquarters plants per m of row reduced marketable tuber yield, marketable number, total yield, and total tuber number by 49, 43, 42, and 31%, respectively (Table 2.7). The reduction in yield and size indicates tuber initiation of potatoes in competition with common lambsquarters was decreased. When removed by 20-cm potato height, competition with summer annuals at 1 to 5 plants m^{-2} (mainly common lambsquarters) did not decrease yield of ‘Mirta,’ a yellow flesh cultivar (Ciuberkis et al. 2007).

Potatoes grown with giant foxtail and hairy nightshade experienced a decrease in marketable tubers and an increase in undersized tubers compared to the weed-free potatoes, which resulted in a similar number of total tubers produced. Nelson and Thoreson (1981) also observed yield reductions and similar tuber number when potatoes were grown in competition with weeds. This may indicate a similar number of tubers were initiated, but tuber bulking was less when potatoes were competing with weeds, which is supported by the undersized tuber number (Table 2.7). Giant foxtail and hairy nightshade competition resulted in undersized tuber

number similar to the weed-free plots. Competition with common lambsquarters reduced tuber initiation and bulking; 42% of tubers were undersized in the common lambsquarters plots, averaged over compost treatments. However, potatoes under common lambsquarters competition produced similar a similar number of undersized tubers to the weed-free plots.

Effect of Compost on Potatoes. Compost did not affect height but influenced fresh vine biomass accumulation ($P \leq 0.1$) at 14, 28, and 42 DAC (Figure 2.3 a-d). Potato vine biomass accumulation was negligible at 56 DAC, which coincided with tuber bulking (Figure 2.1 d). Potatoes grown under $8000 \text{ kg C ha}^{-1}$ compost produced the greatest or equivalent to the greatest fresh vine biomass. Differences in early season biomass may have increased photosynthate production during the tuber bulking phase, resulting in a yield increase (Miller and Hopkins 2008). During this stage, tubers become the prominent sink for photosynthate, and vine growth slows drastically. Potato fresh vine biomass was very low at the end of the season because the crop had achieved physiological maturity and the vines senesced.

Compost did not affect oversized tuber production, cull tuber production, or incidence of hollow heart, vascular discoloration, and bacterial canker (data not presented). Marketable and total yield was lowest when no compost was applied (Table 2.7), and adding $8000 \text{ kg C ha}^{-1}$ increased marketable and total yield over the non-amended by 14 and 12%, respectively. However, the number of marketable and total tubers did not increase, indicating the yield difference observed was due to larger tubers being produced in the composted treatments. Specific gravity of marketable tubers decreased where compost was added (Table 2.7).

To explain the difference in yield observed in the compost treatments, soil moisture was measured in 2011 to quantify water availability. Volumetric water content varied by 1-4% at

Figure 2.3. Potato vine biomass as affected by compost application at (a) 14, (b) 28, (c) 42, and (d) 56 days after potato cracking (DAC). Letters denote differences between compost rates. Bars on the graph depict one standard error of the mean. P-value is the compost rate effect on potato vine biomass.

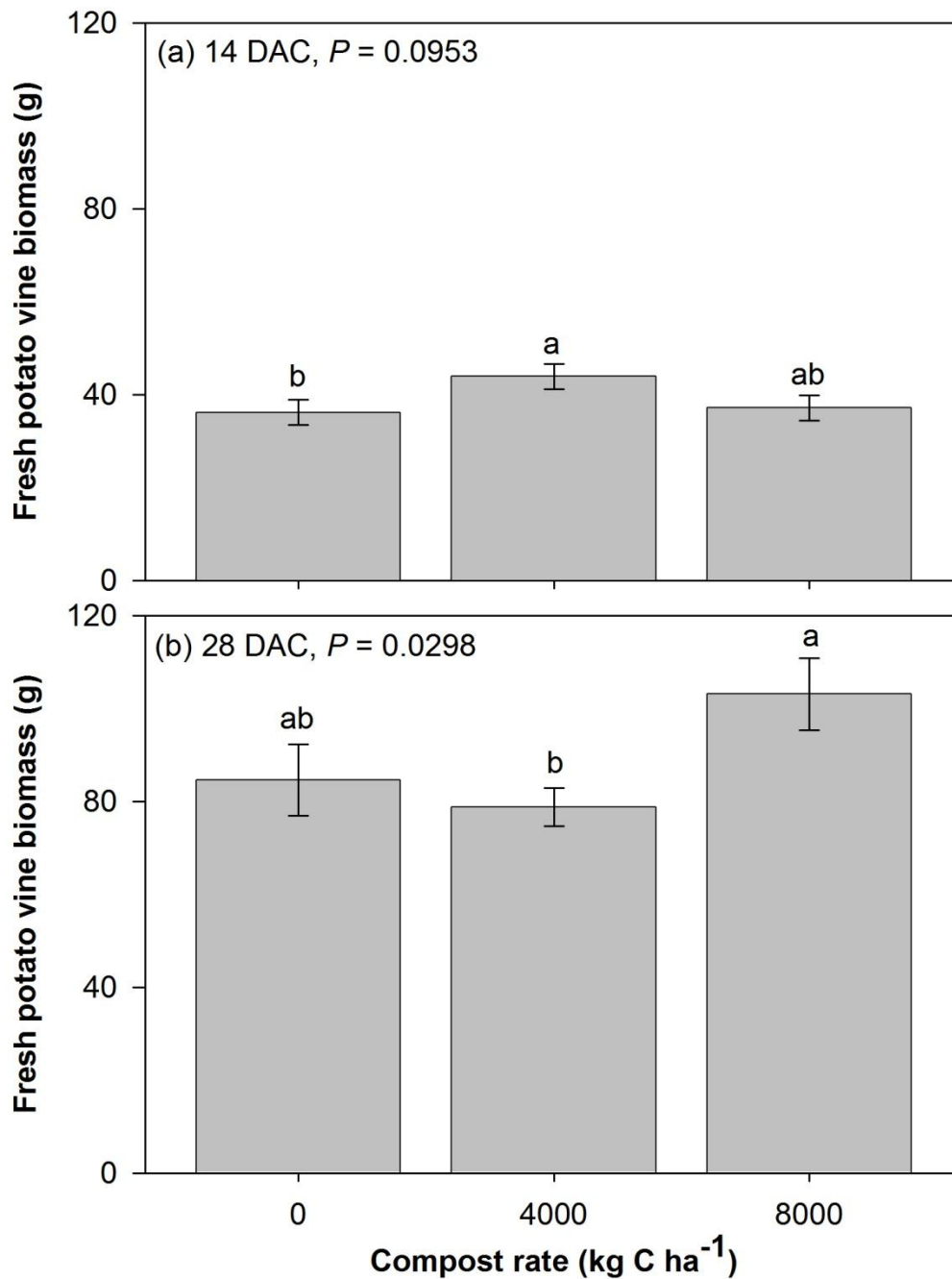
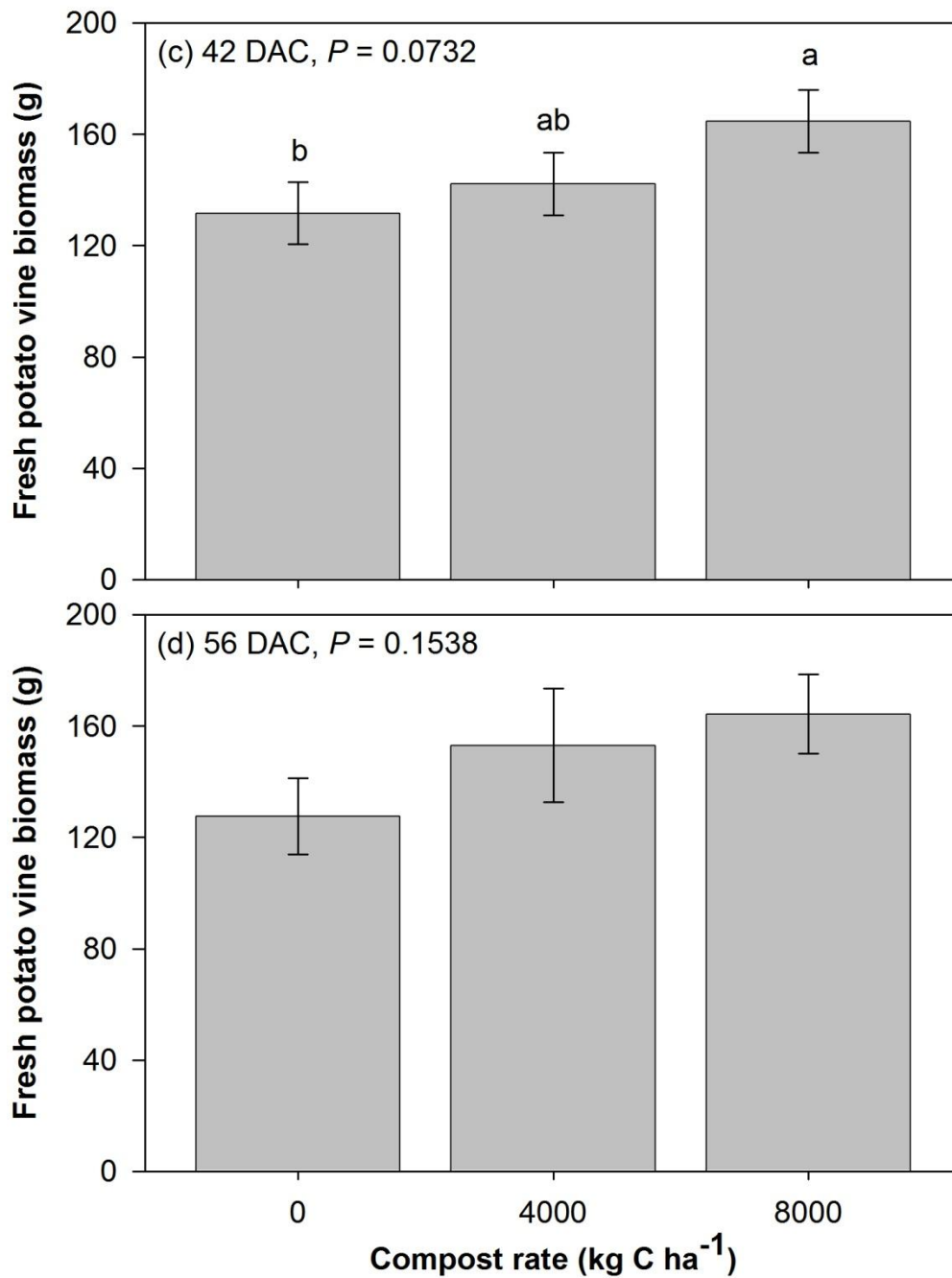


Figure 2.3 (cont'd).



each date because of compost application, and ranged from 4 to 12% at each sampling time. We found no difference in soil volumetric water content in the compost versus non-compost amended treatments ($P \leq 0.05$), suggesting that increased water availability in the composted

treatments was not the reason for increased potato yield. Bulk density may have also affected tuber bulking. If bulk density is decreased because of compost, tuber expansion may have been less restricted during the bulking phase allowing for larger tubers to be produced. Compost effects on bulk density were not measured in this study, but Porter et al. (1999) observed no difference in bulk density in the first year after application of organic amendments (22 t ha⁻¹ waste potato compost plus 45 t ha⁻¹ cattle manure), but after three annual applications bulk density decreased. Additionally, Superior potato yield increased by up to 28%, and specific gravity decreased when amended with 22 t ha⁻¹ waste potato compost plus 45 t ha⁻¹ cattle manure. Therefore, the yield variation may have been because of nutrient application.

Soil nutrient availability was measured both years in the weed-free compost and non-compost treatments. Soil pH increased because of compost application, but macronutrient availability was still greatest in the pH range (6.3 to 7.6). Common scab incidence is increased at pH above 5.2, and may explain common scab levels observed in the tubers (Pavlista 2008). Applying N and K increased the number and yield of medium and large tubers, and P application increased the yield of small and medium tubers while decreasing larger tuber yield (Sharma and Arora 1987). In 2011, there was no effect of compost on inorganic-N throughout the growing season. Since N was balanced across compost treatments we would not expect to see differences in inorganic-N by the addition of compost. We did not balance other macro- and micronutrients by applying additional inorganic fertilizers to the non-compost treatment (Table 2.3). S levels in this study were >15 mg kg⁻¹ and should have been sufficient for potato production (Hopkins et al. 2003). Deficiency of Ca can cause internal defects like brown spot (Guenther and Schotzko 2008), but no differences in internal defects were observed. Soil Ca levels were considered

sufficient, soil Mg levels were also above 100 mg kg⁻¹, and micronutrient levels were above levels necessary for adequate supply (Hopkins et al. 2003).

Specific gravity decreased as compost was applied, and previous literature has shown excess K will reduce specific gravity by increasing tuber water content (Laboski and Kelling 2007; McDole et al. 1978; Stark and Westermann 2008; Westermann et al. 1994). Marketable and total yield was increased when compost was applied, and K application has been shown to increase large and medium tuber yield and decreases small tuber yield (Grewal and Trehan 1993; Kanzikwera et al. 2001; Sharma and Arora 1987; Tawfik 2001).

Conclusions. Compost application in irrigated potatoes receiving supplemental N fertilizer did not increase the competitive ability or seed production of summer annual weeds. Common lambsquarters, giant foxtail, and hairy nightshade at five weeds per m of row across compost rates reduced marketable yield by 49, 17, and 22%, respectively, and must be controlled early in the season to minimize yield loss. Potatoes may benefit from compost amendments because of increased K availability and the potential to increase tuber yield. Potato growers may be able to apply cured composted dairy manure to production fields without increasing the competitive ability of summer annual weeds.

Sources of Material

¹ University Farms, Michigan State University, East Lansing, MI 48824.

² K-Mag Fertilizer, The Mosaic Company, Atria Corporate Center, Suite E490, 3033 Campus Drive, Plymouth, MN 55441.

³ Blend of 28% Urea and Ammonium Nitrate and Liquid Ammonium Phosphate, PotashCorp, Suite 400, 1101 Skokie Blvd, Northbrook, IL 60062.

⁴ Blend of 28% Urea and Ammonium Nitrate and Liquid Ammonium Phosphate, PotashCorp, Suite 400, 1101 Skokie Blvd, Northbrook, IL 60062.

⁵ 28% Urea and Ammonium Nitrate, PotashCorp, Suite 400, 1101 Skokie Blvd, Northbrook, IL 60062.

⁶ Urea, Agrium, Inc, 13131 Lake Fraser Drive SE, Calgary, Alberta T2J7E8.

⁷ Lorox®, Tessenderlo Kerley, Inc, 55 N. 44th Street, Suite 300, Phoenix, AZ 85008.

⁸ Dual II Magnum®, Syngenta Crop Protection, Inc, P.O. Box 18300, Greensboro, NC 27409.

⁹ TeeJet® Technologies, 1801 Business Park Drive, Springfield, IL 62703.

¹⁰ Reinke Single-Gun Lateral Irrigator, Reinke Manufacturing Company, Inc, 5325 Reinke Road, Deshler, NE 68340.

¹¹ Bravo WeatherStik®, Syngenta Crop Protection, Inc, P.O. Box 18300, Greensboro, NC 27409.

¹² Tanos®, E.I. du Pont de Nemours and Company, 1007 Market Street, Wilmington, DE 19898.

¹³ Manzate® Pro-Stick™, E.I. du Pont de Nemours and Company, 1007 Market Street, Wilmington, DE 19898.

- ¹⁴ Admire® Pro™, Bayer CropScience LP, P.O. Box 12014, 2 T.W. Alexander Drive, Research Triangle Park, NC 27709.
- ¹⁵ Radiant® SC, Dow AgroSciences LLC, 9330 Zionsville Road, Indianapolis, IN 46268.
- ¹⁶ Dimethoate 4E, Arysta Lifescience North America, LLC, 15401 Weston Parkway, Suite 150, Cary, NC 27513.
- ¹⁷ Agri-Mek® 0.15EC, Syngenta Crop Protection, Inc, P.O. Box 18300, Greensboro, NC 27409.
- ¹⁸ Agronomy Farm - October 2006, East Lansing, MI 48824.
- ¹⁹ Agronomy Farm - October 2007, East Lansing, MI 48824.
- ²⁰ Field Collected - October 2009, Lakeview, MI 48854.
- ²¹ 25mm Ellepot in Blackmore 105/27 Ellepot tray, Ellepot USA/Blackmore Company, Inc, Belleview, MI 48111.
- ²² FieldScout TDR 300 Soil Moisture Meter, Spectrum Technologies, Inc, 12360 South Industrial Drive East, Plainfield, IL 60585.
- ²³ Rely 200®, Bayer CropScience LP, P.O. Box 12014, 2 T.W. Alexander Drive, Research Triangle Park, NC 27709.
- ²⁴ SAS® 9.2 Software, SAS Institute Inc, 100 SAS Campus Drive, Cary, NC 27513.

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CHAPTER 3

Nutrient Concentration in Weeds and Potato as Affected by Arbuscular Mycorrhizal Fungi

Introduction

Arbuscular mycorrhizal fungi (AMF) are mutualistic organisms that form associations with 90% of plant species (Smith and Smith 2012). Many of the fungi that form AMF associations in cropping systems are *Glomus* spp. Plant nutrient uptake may increase in the presence of AMF [phosphorus (P) and occasionally nitrogen (N)] in exchange for photosynthates. Due to inhibited AMF root colonization (Smith and Read 2008), an AMF inoculum response is unlikely at extractable soil P levels above 50 (Thingstrup et al. 1998) to 140 mg kg⁻¹ (Amijee et al. 1989). Excessive soil P levels decrease hyphae and tube development in spores, and may also inhibit production of the AMF branching factor signaling chemical (Smith and Smith 2012).

Many weedy plant species form associations with AMF. Above-ground biomass was positively correlated with AMF colonization in nine weed species (Bilalis et al. 2011). Black nightshade (*Solanum nigrum* L.) and giant foxtail (*Setaria faberi* Herm.) are two common weeds in Michigan potato production systems that are colonized by AMF while common lambsquarters (*Chenopodium album* L.) is a non-host species (Jordan and Huerd 2008; Vatovec et al. 2005). Vatovec et al. (2005) observed positive mycorrhizal effects for black nightshade and giant foxtail in one of two greenhouse experiments with soil containing 11 to 28 mg kg⁻¹ extractable P, but weeds responded negatively in the second experiment. Colonization of black nightshade and green foxtail [*Setaria viridis* (L.) P. Beauv.] by AMF reduced total biomass after 84 days in another greenhouse study (Veiga et al. 2011) in soil at 10 mg kg⁻¹ extractable P.

Following a fungicide application, AMF colonization of black nightshade decreased and biomass increased in soils containing 33 mg kg^{-1} extractable P (Jordan and Huerd 2008). The negative response may be due to reduced direct root uptake of P from the soil when inadequate levels of AMF colonization occurs (Smith and Smith 2012). These studies suggest that in certain management systems, weeds that form associations with AMF may experience biomass reduction in conjunction with increased nutrient uptake.

Potatoes may form AMF associations (Gerdemann 1968), and yield increases were variable when inoculated with a single isolate of AMF or a mixture of species (Vosátka and Gryndler 2000). Inoculation with *Glomus fasciculatum* but not *G. mosseae* increased yield (Graham et al. 1976). Even within a species of AMF (*G. intraradices*), plant response may vary as tuber yield of ‘Golden Harvest’ decreased but minituber yield increased for the ‘Atlantic’ cultivar (Duffy and Cassells 2000; Niemera et al. 1995). Field grown ‘Superior’ potatoes with 10 to 20% AMF colonization had a 33 to 45% yield increase in high P soils (375 mg kg^{-1}) (Douds et al. 2007). However, in a second experiment there was no yield increase from AMF inoculation. Atlantic potato minitubers in the greenhouse had less than 1% colonization when P was applied weekly (180 g L^{-1} P nutrient solution), but tuber yield was 48-85% greater when grown in the presence of AMF inoculum (Niemera et al. 1995). Other studies with microplants in culture vessels and pre-nuclear minitubers in shade houses have shown increased yield in the presence of AMF inoculum in a low P environment ($<20 \text{ mg kg}^{-1}$) or in growth media, respectively (Davies et al. 2005; Ryan et al. 2003). Unlike the weeds commonly found in Michigan potato fields, potato biomass reductions were not observed after forming an AMF association.

Potato growers in Michigan have shown interest in using commercial AMF inoculum products to improve productivity. Soil P levels in Michigan are typically higher than in other parts of the country ($>100 \text{ mg kg}^{-1}$ extractable P), but benefits from AMF colonization have been observed in potatoes at 375 mg kg^{-1} P (Douds et al. 2007). Potato production in Michigan requires soil P levels near 75 mg kg^{-1} (Warncke et al. 2009). If growers can maximize use of existing soil P with AMF while decreasing weed biomass, potato production and weed management may improve. Alternatively, non-mycorrhizal species like common lambsquarters may become more competitive in potato cropping systems. Previous researchers have recommended controlling weeds after 60% emergence or by 20 cm tall potatoes (Ciuberkis et al. 2007; Felix et al. 2009). Weeds may be less competitive if weed biomass accumulation is delayed because of AMF colonization. Conversely if AMF colonization increases nutrient uptake, weeds may be more competitive in low P environments. Although there has been evidence that AMF can transfer N to the plant, improved N uptake may not affect plant tissue total N content (Douds et al. 2007; Smith and Read 2008).

In addition, AMF may increase plant uptake of important inorganic micronutrients like zinc (Zn) and copper (Cu) (Smith and Read 2008). Zn and boron (B) are involved with hormone regulation of indole acetic acid and auxin accumulation (Puzina 2004), enzyme activity, and protein synthesis (Shashidhar 2006). B is involved in cell wall stability, more so in dicotyledonous plants than grasses (Epstein and Bloom 2005; Havlin et al. 2005). Cu is an important component of enzymes involved in plant metabolism (Shashidhar 2006), and can affect cell membrane lipid structure (Havlin et al. 2005). Manganese (Mn) is an important component of enzymes involved with lignin production (Havlin et al. 2005), the citric acid cycle,

and plant defense (Shashidhar 2006). Iron (Fe) is also a component of plant defense molecules and enzymes, chlorophyll production, and ATP synthesis (Epstein and Bloom 2005). The health of plants with AMF associations may improve if micronutrient uptake is elevated, resulting in more competitive plants.

AMF may also influence water relations as increases in plant growth may be due to increased nutrient availability from increased water uptake (Smith and Read 2008). Shantz and Piemeisel (1927) observed similar water use efficiency values for two C₃ weeds [i.e., common lambsquarters and cutleaf nightshade (*Solanum triflorum* Nutt.)] and the C₃ potato (1.5-2.0 mg dry weight g⁻¹ water). The leaf water use efficiency of common lambsquarters and C₄ giant foxtail at 300 ppm CO₂ levels were 4.6 and 12.9 mg CO₂ g⁻¹ water, respectively (Carlson and Bazzaz 1982). If the AMF host plants form associations with AMF, uptake of nutrients from the soil may increase relative to common lambsquarters because of increased water use efficiency.

There is no published research concerning the use of AMF in the ‘Snowden’ variety potato (a common white round cultivar in Michigan). AMF colonization of potato and weedy species, and the resulting changes in plant biomass and nutrient concentration, could influence the competitiveness of weeds in potato production systems. The objectives of this study were to investigate the effects of AMF inoculation on plant growth, plant development, root colonization, nutrient concentration, and nutrient use efficiency.

Materials and Methods

A greenhouse study was conducted in July and August of 2011 at Michigan State University in East Lansing, MI, using a split-plot completely random design. Each treatment

was replicated four times, and the experiment was repeated in time. A mixture of Riddles sandy loam (fine-loamy, mixed, active, mesic Typic Hapludalfs) and Hillsdale sandy loam (coarse-loamy, mixed, active, mesic Typic Hapludalfs) field soil (Table 3.1) collected to 20-cm depth was passed through a 6-mm sieve and steam autoclaved at 110°C and 140 kPa for 16 h to sterilize the soil of native arbuscular mycorrhizal fungi (AMF) and plant pathogen populations. Because of documented increases in N and P availability with autoclaving soil (Eno and Popenoe 1964; Ferriss 1984; Heinrich and Patrick 1986), soil was analyzed for nutrient content after autoclaving. Soil ranged from 79 to 91 mg P kg⁻¹ soil (Table 3.1), which exceeded the critical soil P level for potato production in Michigan (75 mg kg⁻¹). Soils with relatively low P levels were used to stimulate AMF colonization due to soil P being relatively immobile in the soil (Havlin et al. 2005).

Table 3.1. Initial soil properties for both runs of this experiment.^a

	pH	Organic Matter	Inorganic-N	P	K	Mg	Ca
		%		mg kg ⁻¹			
Run 1	5.8	2.0	6.51	79	187	115	620
Run 2	6.0	2.0	5.27	91	193	103	591

^a Abbreviations: N, nitrogen; P, phosphorus; K, potassium; Mg, magnesium; Ca, calcium.

Soil was cooled for 20 h after autoclaving and treated with a commercially available AMF product¹ at one of four rates: 0, 0.3, 0.6, 1.2 g L⁻¹ soil equivalent to 0, 1, 2, and 4x the recommended rate for planting soil. The product consisted of a guaranteed analysis of at least 67 propagules g⁻¹ each of *Glomus aggregatum* Schenk & Smith, *G. etunicatum* Becker & Gerdemann, *G. intraradices* Schenck & Smith, and *G. mosseae* (Nicol. & Gerd.) Gerd. & Trappe. Twelve-liter pots were initially filled to volume (11.3 L soil), and the soil was poured into a separate container and inoculated by thoroughly mixing one inoculum rate throughout the

soil. AMF inoculum was homogenized throughout the pot based on recommended application method. Soil was not stratified within the pot by collection depth to mimic a homogenized plow layer that would be present at potato planting. Paper was placed inside the pot to allow for drainage while preventing soil loss. The inoculated soil was added back into the pot containing at least 0, 910, 1,820, or 3,630 propagules of AMF. The pots were watered to field capacity and randomly arranged within a species under natural light (13 to 14 hr day/10 to 11 hr night) in the greenhouse. Temperature in the greenhouse was maintained at day/night temperatures of 29/24°C.

One uncut potato seed-piece (Snowden cultivar, 40 to 50 g for Run 1 and 55 to 65 g for Run 2) was planted 2.5-cm deep. Hairy nightshade seeds² were soaked in 2 g L⁻¹ gibberellic acid for 24 h at 22°C to stimulate germination (Spicer and Dionne 1961; Edmonds 1986), while seeds from giant foxtail³ and common lambsquarters⁴ were acclimated in the dark for 24 h at 22°C. Four to ten seeds of each weed species were planted per pot 1-cm deep, and emerging plants were thinned to one plant per pot. Pots were watered as needed to maintain adequate soil moisture. Pots were not fertilized in an attempt to induce nutrient stress and AMF colonization.

Leaves of weeds and potato were counted and plant heights measured weekly for seven weeks after planting. Whole plants were harvested 42 days after planting (DAP) and separated into above- and below-ground samples and weighed. Due to tuber seed-piece rot from internal fungi, three replications of potato biomass were harvested from each run. Potato above-ground biomass was calculated by dividing biomass by the number of stems harvested. Above-ground biomass was dried for 4 d at 60°C, weighed, and two plants from each treatment were ground

and tissue analyzed for nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), sulfur (S), boron (B), zinc (Zn), manganese (Mn), iron (Fe), and copper (Cu) . The percent of each nutrient in the tissue was multiplied by the dry above-ground biomass to obtain g nutrient per plant. Nutrient use efficiency was calculated by dividing total dry above-ground biomass by the g nutrient per plant.

Below-ground material (roots) was washed, cut into 1-cm segments, and preserved in 50% ethanol until tested for mycorrhizal colonization (Brundrett et al. 1996). Below-ground root segments were stained according to the procedure by Grace and Stribley (1991). Roots were cleared in 10% KOH and stained with aniline blue (in acidified glycerol). Five root segments of a sample were wet mounted onto a microscope slide, and two slides were prepared per sample. To estimate root colonization by arbuscular mycorrhizae, slides were scanned at 200x magnification using a transmitting light microscope and hyphae, arbuscules, and vesicles were counted using the magnified colonization intersections method (McGonigle et al. 1990).

Statistical Analysis. Data were analyzed using a one-way ANOVA with the MIXED procedure in SAS® 9.2⁵. Inoculum rate, plant species, and their interaction were treated as fixed factors, with run and replication as random factors. Normality of the residuals was evaluated by visual examination of normal probability and stem-and-leaf plots. Homogeneity of the variances was evaluated by residual plots, box plots, and Levene's test ($\alpha = 0.1$) and grouped to reduce the AIC value of the model using the GROUP option of the REPEATED statement. When the interaction between inoculum rate and weed species was found to be significant ($\alpha = 0.05$), comparisons between the combinations at each compost rate and weed species level were examined by slicing and conducting individual pair-wise comparisons using t-tests. When factors were found to be

significant ($P \leq 0.05$), all-pairwise comparisons were conducted using Fisher's protected LSD. The PROC REG procedure was used to fit a linear regression model to examine the relationship of tissue nutrient levels and inoculum rate, and the regression equations and R^2 values were reported. A model was considered significant if the global F-test was significant at $\alpha = 0.05$. The PROC CORR procedure was used in SAS to correlate dry above-ground biomass and fresh below-ground biomass with percentage nutrient in the plants. A significant correlation was present if $P \leq 0.05$, and the Pearson correlation coefficient (r) was reported.

Results and Discussion

In a preliminary study where soil P was $\geq 125 \text{ mg kg}^{-1}$, there were no differences in above- or below-ground plant biomass for any plant species regardless of inoculum rate (data not presented). High soil P content can decrease AMF colonization and hyphal growth and development (Smith and Read 2008). Therefore the experiment was repeated twice at soil P levels of 79 to 91 mg kg^{-1} extractable P. This value is above the critical level of 75 mg kg^{-1} extractable P needed for potatoes grown in Michigan (Warncke et al. 2009).

Mycorrhizal Effect on Plant Growth.

Potatoes. Potato roots were not colonized by AMF (data not presented), and there were no differences ($P \leq 0.05$) 42 DAP in height, above- or below-ground biomass, or tuber development (Tables 3.2 and 3.3). Potatoes were harvested at the beginning of the bulking phase (42 DAP), which coincides with phloem-mobile nutrients (like N and P) being transported from the vines to the tubers during tuber bulking (Miller and Hopkins 2008). If AMF had assisted with N and P

Table 3.2. Plant growth as affected by inoculum rate.^a

Species	Inoculum	Height	Flower	FAB	FBB	DAB
	g L ⁻¹ soil	cm	%	g		
CHEAL	0.0	87.8	100	62.23	24.35	9.56
	0.3	87.9	87.5	57.17	14.46	7.93
	0.6	92.8	75.0	53.54	20.68	8.03
	1.2	91.1	87.5	67.72	22.82	10.54
SETFA	0.0	101	100	75.43	33.53	12.03
	0.3	107	100	70.69	23.49	10.99
	0.6	117	100	80.99	23.20	13.98
	1.2	111	100	89.08	33.37	14.74
SOLSA	0.0	39.6	87.5	100.48	7.55	7.51
	0.3	41.9	87.5	106.09	12.45	8.56
	0.6	44.3	100	116.81	14.88	11.13
	1.2	43.9	100	124.57	8.87	11.58
potato	0.0	51.9	90.1	122.77	24.28	12.94
	0.3	63.3	80.4	135.94	27.41	14.46
	0.6	58.9	90.4	121.35	24.10	13.69
	1.2	53.7	39.9	122.06	22.93	12.76
LSD (0.1) ^b		n.s.	30.8	n.s.	13.40	n.s.

^a Abbreviations: FAB, fresh above-ground biomass; FBB, fresh below-ground biomass; DAB, dry above-ground biomass; CHEAL, common lambsquarters; SETFA, giant foxtail; SOLSA, hairy nightshade.

^b Means within a column greater than the least significant difference (LSD) value are different from each other; n.s. indicates that treatments were not different from each other.

Table 3.3. Potato tuber production as affected by inoculum rate.

Inoculum Rate	Tuber number	Tuber weight	Average weight per tuber
g L ⁻¹ soil		g	
0.0	4.26	13.52	3.17
0.3	4.81	15.60	3.24
0.6	3.29	11.24	3.42
1.2	2.49	2.07	0.83
LSD ^a (0.05)	n.s.	n.s.	n.s.

^a Means within a column greater than the LSD value are different from each other; ; n.s. indicates that treatments were not different from each other.

uptake, benefits should be realized from emergence to the bulking phase. While fertilizer was not used in this experiment and potatoes did not exhibit N deficiency symptoms until harvest, applying N fertilizer at planting may have stimulated root growth (Stark and Westermann 2008)

and increased colonization incidence. Pre-nuclear potato minitubers grown in highly fertilized inoculated peat-based media had less than 1% root colonization (Niamera et al. 1995), and Douds et al. (2007) observed no difference in field-grown Superior potato biomass with 10 to 20% root colonization in soils with 375 mg P kg^{-1} soil 42 DAP. Other research has shown biomass of pre-nuclear minitubers increased 90 days after transplanting into soil inoculated with AMF and fertilized with 11 mg kg^{-1} P, but the inoculum effect was eliminated in soils that received 44 mg kg^{-1} P and no inoculum (Davies et al. 2005). Inoculum rates in these previous experiments ranged from 30 to 5400 propagules placed below the seedpiece or as a solid layer within the pot. Colonization in our experiment may not have occurred because the inoculum rates were lower and homogenized throughout the pot, thus eliminating a concentrated AMF source. There has been limited research on AMF inoculation of Snowden potatoes, and yield response to mycorrhizal inoculum is cultivar specific (Vosátka and Gryndler 2000). The delay in flowering (Table 3.2) and tuber development of potatoes under the 1.2 g L^{-1} rate (Table 3.3) is because the potato stage ranged from tuber initiation to tuber bulking (<7 d difference), which is similar to physiological variation in field-grown potatoes. Even if differences in tuber development had been observed at 42 DAP, these differences in tuber growth and development may not have resulted in total tuber yield differences (Duffy and Cassells 2000).

Weeds. Giant foxtail, hairy nightshade, and common lambsquarters also were not colonized by AMF at this level of P (80 mg kg^{-1}) (data not presented). Common lambsquarters is a species that does not form mycorrhizal associations, but giant foxtail and the nightshades are host plants (Jordan and Huerd 2008; Vatovec et al. 2005) and colonization was expected on these species.

Veiga et al. (2011) observed colonization levels of 63 to 80% for green foxtail and black nightshade when grown in soils at 10 mg kg^{-1} extractable P levels; our extractable P was ten-fold greater. The inoculum may have been less concentrated in our study, but neither Veiga et al. (2011) nor Vatovec et al. (2005) report the number of propagules added per pot. Brundrett et al. (1996) suggested colonization may not be an accurate measure of mycorrhizal benefits and other parameters including plant biomass and nutritional content may better quantify mycorrhizal benefits.

Regardless of inoculum rate, there were no differences ($P \leq 0.05$) in height, flowering, above-ground biomass, or below-ground biomass within the three weed species 42 DAP (Table 3.2). A positive correlation between biomass and AMF colonization had been reported when averaged over nine weedy species (Bilalis et al. 2011); however none of these weed species were included in our study. In soils ranging from 11 to 28 mg kg^{-1} P, the biomass of AMF colonized giant foxtail and black nightshade plants was less than the non-inoculated control in one of two experiments (14 to 45% decrease), but the opposite trend (-1 to 24% increase) occurred in the second experiment (Vatovec et al. 2005). Twelve weeks after planting, plant biomass of green foxtail and black nightshade decreased by 30% when colonized by AMF in soils with P levels at 10 mg kg^{-1} (Veiga et al. 2011), suggesting a non-symbiotic relationship between AMF and these weedy species.

Previous studies have observed a variable relationship between percent colonization and plant growth. Because there was no colonization and no effect of inoculum on biomass, it is likely colonization did not occur in this study. The soil P levels ($79 \text{ to } 91 \text{ mg kg}^{-1}$) may have been too great to observe colonization. At levels above $50 \text{ to } 140 \text{ mg kg}^{-1}$ extractable P, an

inoculation response to AMF is unlikely to occur (Amijee et al. 1989; Thingstrup et al. 1998). Another possible reason is the inoculum was not concentrated below the seed. Previous studies applied the inoculum as a band below the seed, and we incorporated the inoculum throughout the pot based on application recommendation. Many studies also observe mycorrhizal effects only after 80 days or more of growth (Davies et al. 2005; Douds et al. 2007; Jordan and Huerd 2008), suggesting that plants in our greenhouse study may have been harvested prior to AMF colonization.

Nutritional Content as Affected by Mycorrhizal Inoculum. Nutrient content within potatoes or weeds was not affected by inoculum rate (Figures 3.1 a-f and 3.2 a-e), and regression analysis revealed R^2 values <0.4 for all nutrients and species. Interactions of species and inoculum rate occurred in the percentage N in above-ground biomass of hairy nightshade and the percentage B in above-ground common lambsquarters biomass; however, the interaction may have been the result of a dilution factor where larger plants contain a smaller overall percentage of the nutrient (Blackshaw et al. 2003). The percent nutrient within the above-ground tissue was negatively correlated with dry above-ground biomass for most nutrients; as dry above-ground biomass increased the percent nutrient in the tissue decreased, indicating the dilution effect (Table 3.4). To account for this effect, nutrient content in mg nutrient per plant and nutrient use efficiency of the weeds and crop are also reported (Table 3.5).

There were few differences in macronutrient content per plant of the four species in our research (Table 3.5). Potatoes had more Ca per plant than other species as potatoes accumulate calcium in the above-ground tissue for use during tuber bulking (Guenther and Schotzko 2008).

Figure 3.1. Arbuscular mycorrhizal fungi inoculum did not influence the elemental analysis of common lambsquarters (CHEAL), giant foxtail (SETFA), hairy nightshade (SOLSA), and potato for (a) nitrogen, (b) phosphorus, (c) potassium, (d) magnesium, (e) calcium , and (f) sulfur.

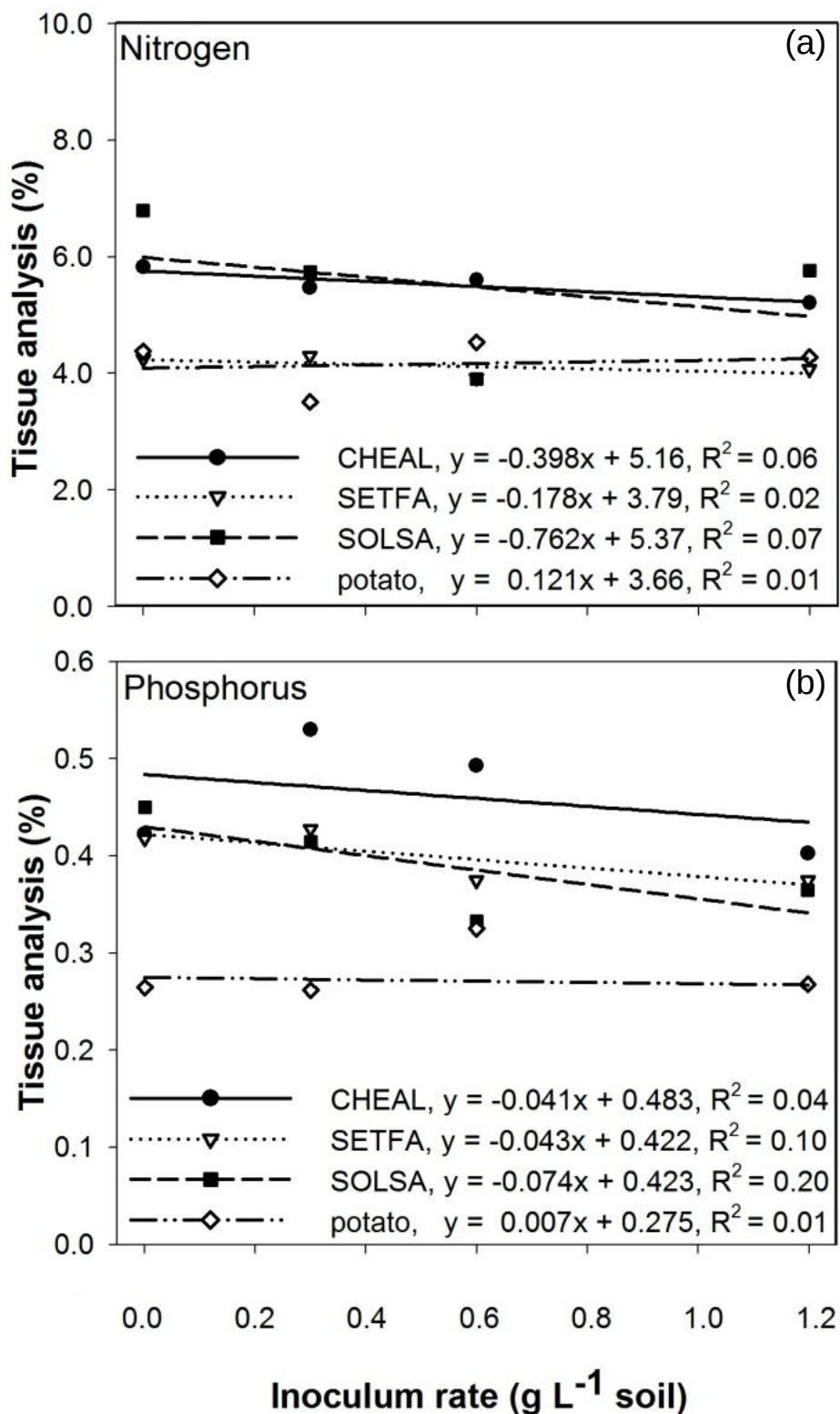


Figure 3.1 (cont'd).

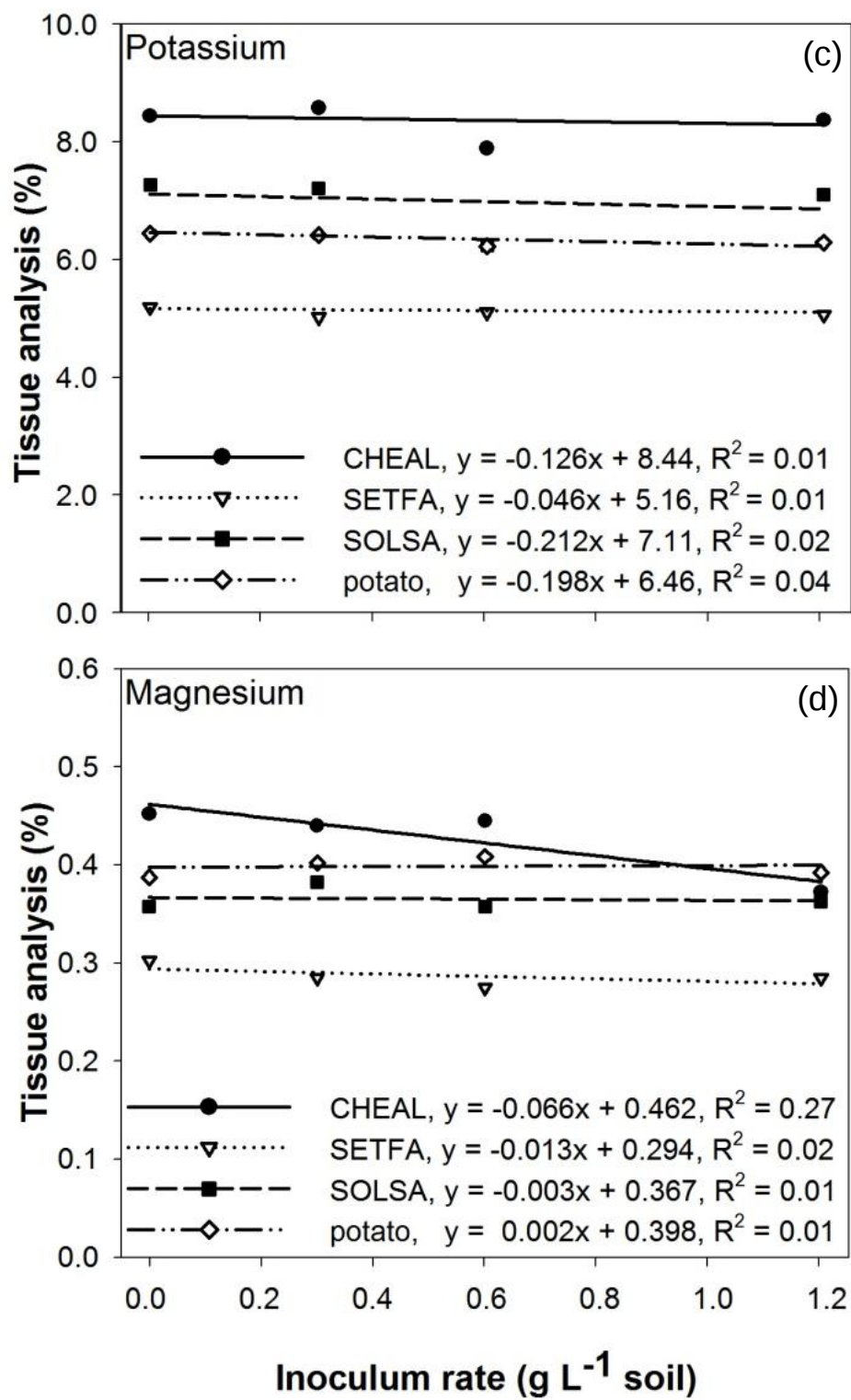


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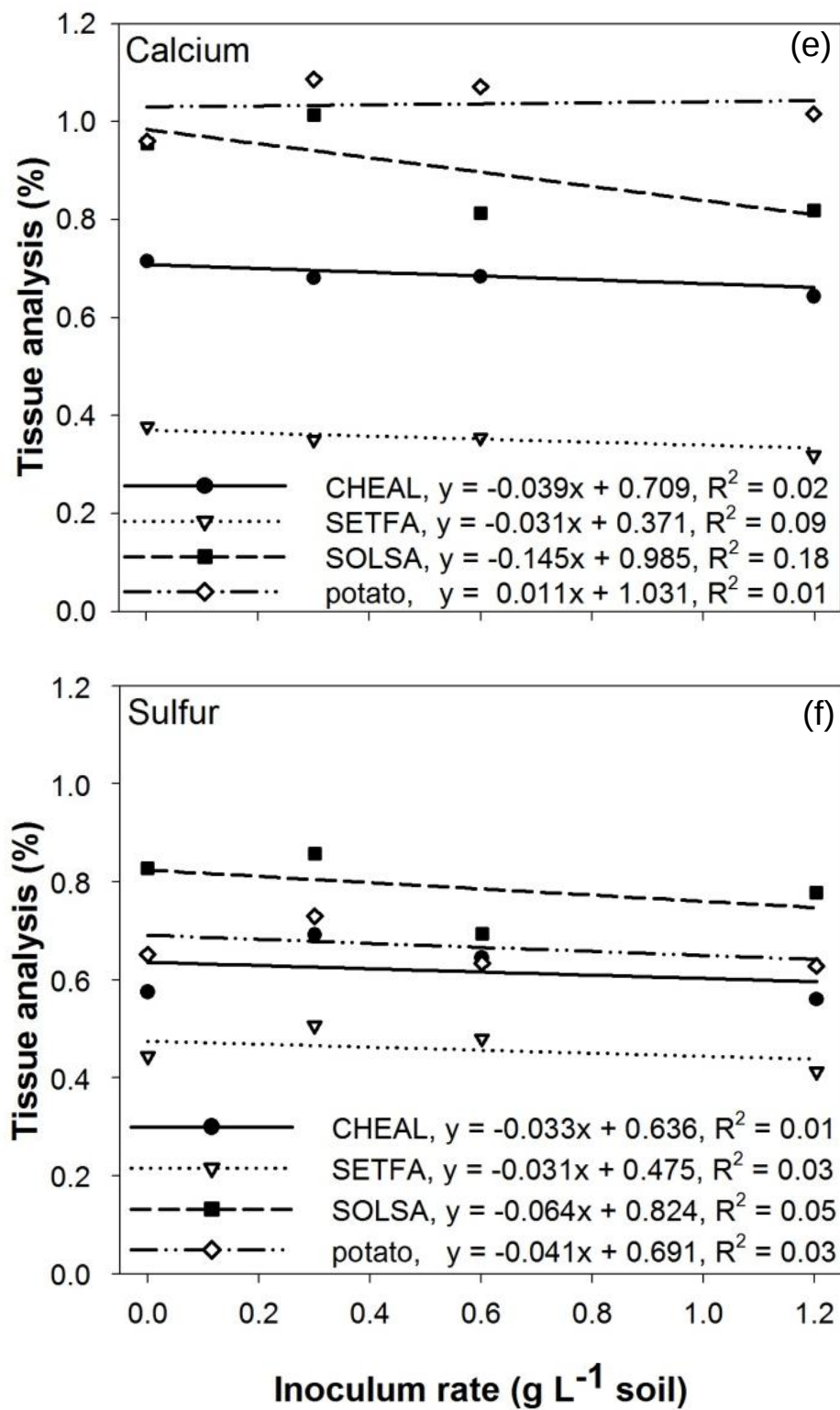


Figure 3.2. Tissue concentration of (a) boron, (b) manganese, (c) zinc, (d) copper, and (e) iron for common lambsquarters (CHEAL), giant foxtail (SETFA), hairy nightshade (SOLSA), and potato was not influenced by arbuscular mycorrhizal fungi inoculum.

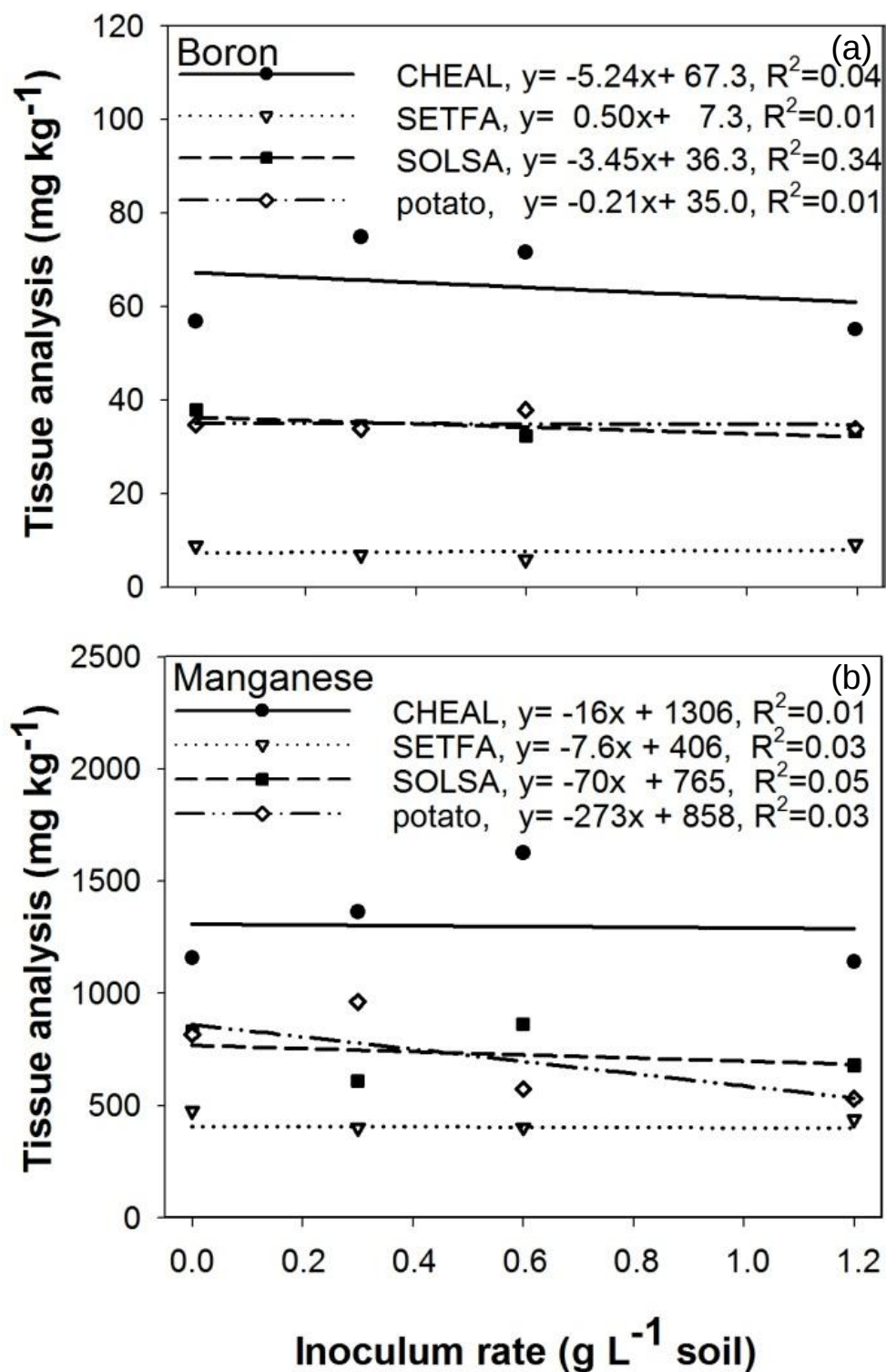


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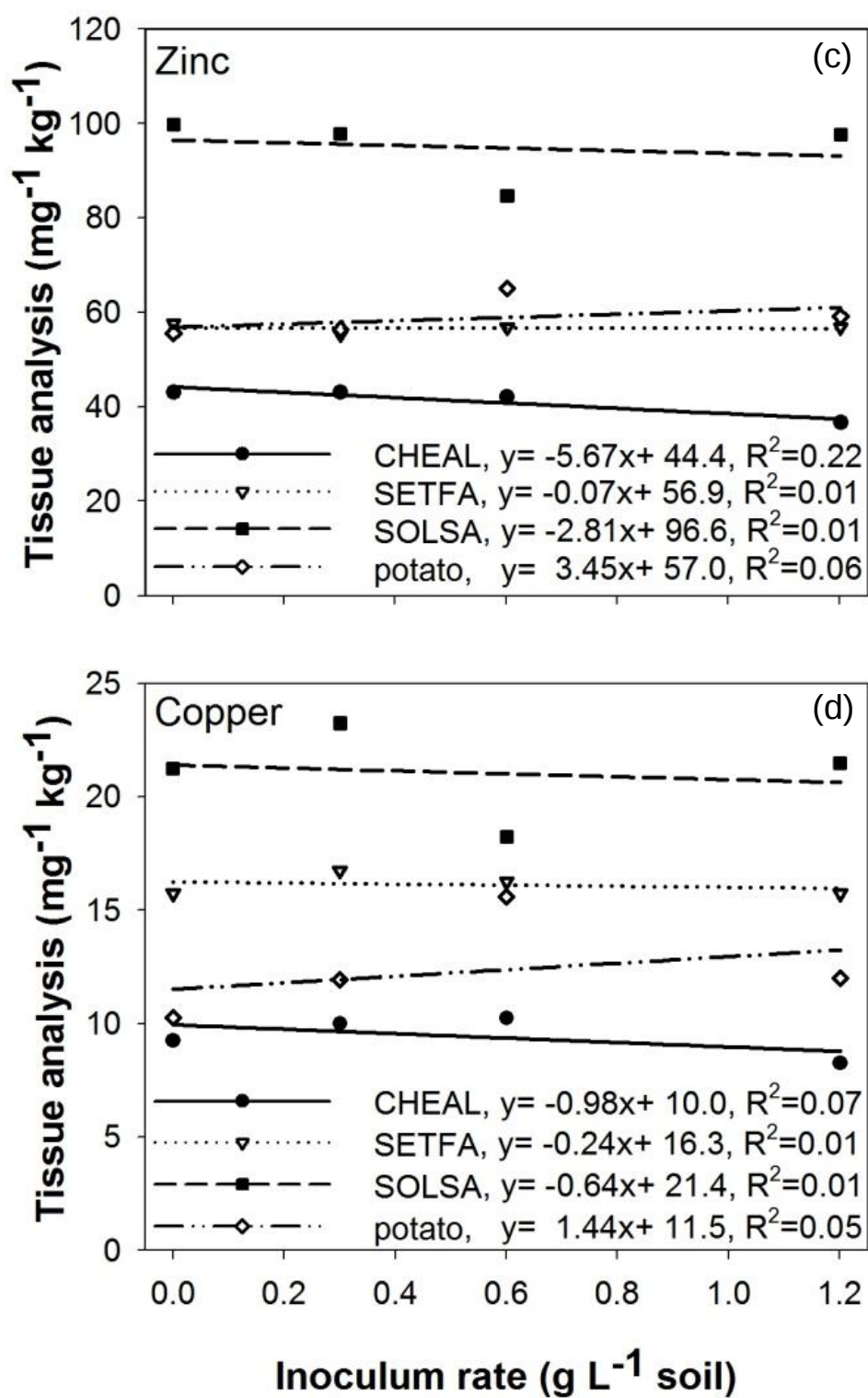


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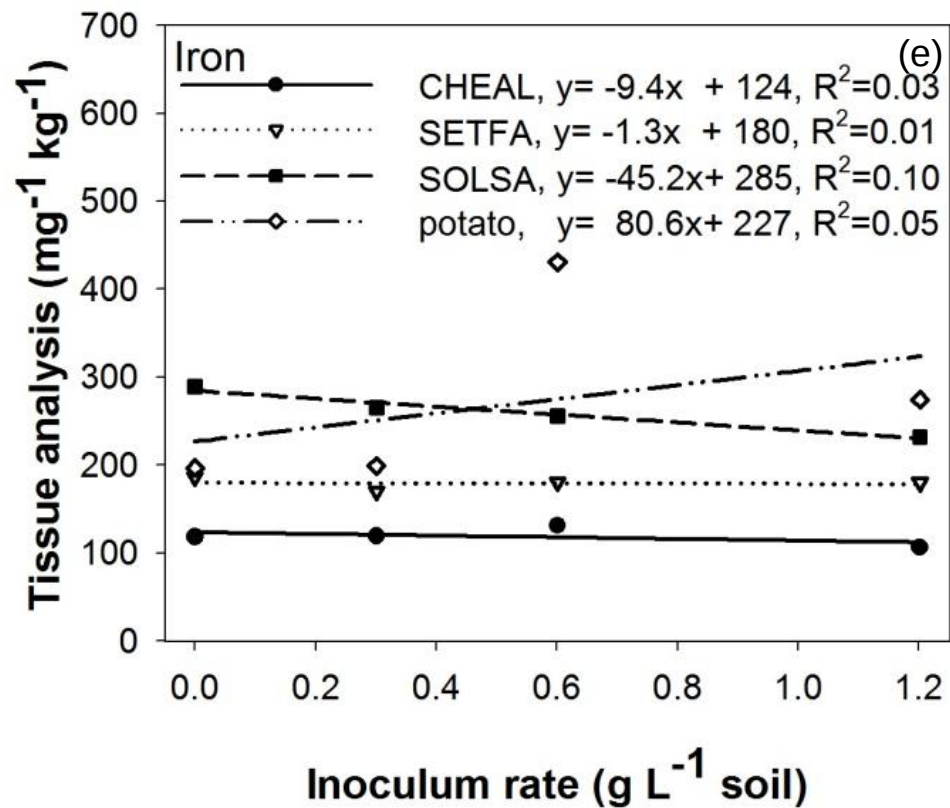


Table 3.4. Pearson correlation coefficients (r) of nutrients with plant biomass.^{a,b}

Macronutrient	DAB	FBB	Micronutrient	DAB	FBB
N	-0.783***	-0.565***	B	-0.443***	-0.194
P	-0.661***	-0.212	Zn	-0.218	-0.513***
K	-0.574**	-0.348**	Mn	-0.298*	-0.019
Mg	-0.298*	-0.030	Fe	-0.161	-0.316**
Ca	-0.152	-0.318*	Cu	-0.235	-0.388**
S	-0.430***	-0.469***			

^a Abbreviations: DAB, dry above-ground biomass; FBB, fresh below-ground biomass; N, nitrogen; P, phosphorus; K, potassium; Mg, magnesium; Ca, calcium; S, sulfur; B, boron; Zn, zinc; Mn, manganese; Fe, iron; Cu, copper.

^b *** indicates $P \leq 0.001$, ** is $P \leq 0.01$, and * indicates $P \leq 0.05$.

Table 3.5. Nutrient content, concentration, and use efficiency across inoculum for each species.^a

Species	N	P	K	Mg	Ca	S	B	Zn	Mn	Fe	Cu
Nutrient Content (mg nutrient plant ⁻¹)											
CHEAL	488	45.1	735	43.2	68.7	59.9	0.63	0.41	13.5	1.17	0.092
SETFA	502	53.5	690	38.6	47.7	61.0	0.10	0.78	5.9	2.37	0.216
SOLSA	490	39.6	718	37.5	92.2	80.8	0.35	0.97	7.8	2.56	0.214
potato	503	37.9	881	55.9	145	92.2	0.48	0.81	9.9	3.62	0.169
LSD ^b (0.05)	n.s.	19.1	n.s.	n.s.	47.9	n.s.	0.12	0.25	5.0	n.s.	0.078
Tissue Elemental Analysis											
%											
CHEAL	4.95	0.46	8.32	0.43	0.68	0.62	64.6	41.4	1320	120	9.4
SETFA	3.70	0.40	5.09	0.29	0.35	0.46	7.7	56.8	430	180	16.1
SOLSA	4.98	0.39	6.95	0.37	0.90	0.79	34.5	95.1	740	260	21.1
potato	3.74	0.28	6.34	0.40	1.03	0.66	35.1	59.2	720	275	12.4
LSD (0.05)	1.32	n.s.	1.71	n.s.	0.24	0.25	5.9	10.4	480	115	6.5
mg kg ⁻¹											
Nutrient Use Efficiency											
g biomass g ⁻¹ nutrient											
CHEAL	20.7	225	12.1	238	153	168	16.0	24.6	0.84	8.80	109.1
SETFA	27.6	258	20.0	356	289	225	148.7	17.7	2.54	5.97	62.7
SOLSA	21.7	265	14.5	276	115	130	29.2	10.7	1.44	4.13	49.8
potato	27.7	370	15.9	253	97	154	28.6	17.1	1.65	4.70	86.0
LSD (0.05)	8.1	66	n.s.	n.s.	65	53	58.6	n.s.	1.13	3.10	21.6

^a Abbreviations: N, nitrogen; P, phosphorus; K, potassium; Mg, magnesium; Ca, calcium; S, sulfur; B, boron; Zn, zinc; Mn, manganese; Fe, iron; Cu, copper; CHEAL, common lambsquarters; SETFA, giant foxtail; SOLSA, hairy nightshade; LSD, least significant difference.

^b Means within a column greater than the least significant difference (LSD) value are different from each other; n.s. indicates that treatments were not different from each other.

Giant foxtail tissue contained the lowest percentage of macronutrients and the greatest macronutrient use efficiency, which was expected because many C₄ species are more efficient at using nutrients compared to C₃ plants (Brown 1978). Percentage N and N use efficiency in potato was equivalent to the values in giant foxtail, which may indicate N was limited in the system and could have been increased with an N fertilizer application at planting. Potatoes contained the amount of P, but also had improved N and P use efficiency above that of the other C₃ plants. Common lambsquarters and hairy nightshade contained the highest percentage N and

had the lowest N use efficiency of all species examined. Common lambsquarters and hairy nightshade had elevated concentrations of N and P compared to potatoes. The summer annual weeds have a higher relative growth rate than potato and can have greater concentrations of macronutrients relative to potato (DiTomaso 1995). Aside from N and P, the C₃ broadleaf species in this study had similar macronutrient content and use efficiency. Due to nutrient transport in mineral form from the mycorrhizae to the plant, Smith and Read (2008) suggest mycorrhizae increase nutrient uptake because of additional surface area and water uptake. Therefore, the similarities in broadleaf uptake of nutrients may be related to similarities in water use efficiency when compared to C₄ grasses (Carlson and Bazzaz 1982; Norris 1996; Shantz and Piemeisel 1927).

Hairy nightshade and potato accumulated similar concentrations of micronutrients and had similar nutrient use efficiencies (Table 3.5). B and Zn concentrations were inversely related within the potato and weedy species. Furthermore, B levels were lower in the grass species, which is consistent with previous research (Havlin et al. 2005). A similar inverse relationship occurred with Mn and Fe. Total plant content and percentage Cu, important in C and N metabolism (Shashidhar 2006), was lowest in common lambsquarters compared to the other species. However, use efficiency was greatest in giant foxtail or common lambsquarters for most micronutrients examined, and these weeds may be more competitive in soils where micronutrient availability is reduced (higher pH soils). Micronutrient uptake and micronutrient use efficiency was more variable across plant species than for macronutrients, and may affect competition by influencing plant defense, enzyme activity, and hormone regulation.

Management Implications. This greenhouse study suggests mycorrhizal inoculum incorporation may not benefit potatoes or reduce weed growth in Michigan. Additionally, extractable P in soils from most potato production systems is above the critical level needed for potato growth and development. In areas where exchangeable P is below 75 mg kg^{-1} , mycorrhizal inoculation may increase potato growth relative to weeds, but further research (including field trials) are needed to confirm this hypothesis. Plants may have been harvested too soon to observe AMF colonization (many studies observe benefits >80 days), but colonization of potatoes should be expected to present during the tuber initiation and bulking phases when nutrient uptake is greatest.

While mycorrhizal colonization did not occur, differences in nutrient composition of the four plant species were evident. Nutrient percentages were negatively correlated with plant biomass, and percentage differences in nutrient content were reduced when examining total plant content for macronutrients. Summer annual C₃ weeds had greater N concentration than potato. Nutrient use efficiency varied by species, with giant foxtail having the greatest macronutrient use efficiency and common lambsquarters the greatest micronutrient use efficiency. Micronutrient content may affect plant growth rates, hormone regulation, and the competitive ability of weeds. Research altering macronutrient and micronutrient content in soil may be beneficial to further investigate how nutrient content affects the competitive ability of summer annual weeds.

Sources of Material

¹ MycoApply® Ultrafine Endo, Mycorrhizal Applications Inc., Grants Pass, OR 97528.

² Field Collected - October 2009, Lakeview, MI 48854.

- ³ Agronomy Farm - October 2007, East Lansing, MI 48824.
- ⁴ Agronomy Farm - October 2006, East Lansing, MI 48824.
- ⁵ SAS Institute Inc, 100 SAS Campus Drive, Cary, NC 27513.

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CHAPTER 4

Influence of Maternal and Burial Environment on Seed Mortality and Dormancy of Three Summer Annual Weed Species

Introduction

Soil amendments such as compost can increase soil organic matter, water and nutrient holding capacity, soil aggregation, and soil microbial activity (Gonzales and Cooperband 2002; Magdoff and van Es 2000; Salem et al. 2010). Compost has fewer viable weed seeds as compared to fresh manure (Wiese et al. 1998), but both compost and manure can be used as nutrient sources to reduce fertilizer purchases (Menalled et al. 2005a).

Compost amendments may affect soil nutrient availability and water holding capacity in farm fields. These environmental conditions will, in turn, influence seed development, fecundity, dormancy and mortality of seeds produced on the mother plant (e.g., Kegode and Pearce 1998; Kigel et al. 1977; Naylor 1983). The seed coat, which is maternally derived (Bewley and Black 1994), consists of complex carbohydrate molecules like hemicelluloses (Mullin and Xu 2001), a dense layer of lignified cells (Kremer et al. 1984), and secondary phenolic compounds (Mohamed-Yasseen et al. 1994) which act as a defense mechanism. These hemicelluloses can limit seed water uptake (Mullin and Xu 2001), and may provide physical restraints to germination (Schutte et al. 2008). Fenner (1991) found less dormancy in seed produced on maternal plants grown under high temperatures, drought conditions, and high nitrogen.

Seed mortality may also be influenced by the environment in which the seed is buried (Fenner and Thompson 2005), yet the effect of compost on seed persistence has been studied by

few researchers. Composted cattle (*Bos taurus*) manure at 30 t ha⁻¹ did not change the seed-bank of downy brome (*Bromus tectorum* L.), field pennycress (*Thlaspi arvense* L.), or flaxweed [*Descurainia sophia* (L.) Webb ex Prantl] when compared to the seed-bank where broadcasted conventional fertilizer was applied (Blackshaw et al. 2005). Similarly, spring application of 45 t ha⁻¹ beef cattle manure and 22 t ha⁻¹ cull potato compost did not affect weed seed-bank values when herbicides were used for weed control, but reduced seed-bank values when tillage alone was used to control weeds (Gallandt et al. 1998). Composted swine (*Sus scrofa*) manure applied at 4 or 8 t carbon (C) ha⁻¹ did not impact weed seed survival, longevity, or emergence of giant foxtail (*Setaria faberi* Herrm.), common lambsquarters (*Chenopodium album* L.), or common waterhemp (*Amaranthus rudis* Sauer) (Menalled et al. 2005b); however, at higher compost rates (16 and 24 t C ha⁻¹) common waterhemp and giant foxtail emergence was delayed (Menalled et al. 2005a). Composted dairy (*Bos taurus*) manure (18, 36, and 54 t ha⁻¹) also decreased emergence of redroot pigweed (*Amaranthus retroflexus* L.) (Amisi and Doohan 2010). In other research, applications of composted vegetable, fruit, and garden waste applied at 22.5 t ha⁻¹ annually or 45 t ha⁻¹ tri-yearly reduced the seed-bank of common lambsquarters and black nightshade (*Solanum nigrum* L.) (De Cauwer et al. 2009). No studies have examined the effect of compost on hairy nightshade (*Solanum physalifolium* Rusby).

If weed emergence is delayed or seed viability is increased by the addition of compost, the competitiveness of the weeds with potato (*Solanum tuberosum* L.) may be affected. ‘Russet Burbank’ potatoes were more competitive than hairy nightshade regardless of weed emergence timing, but ‘Russet Norkotah’ was less competitive when hairy nightshade emerged prior to

potato in greenhouse experiments (Hutchinson et al. 2011). Delaying weed emergence may increase the competitive ability of potato, but grass and broadleaf weeds emerging up to 25 days after ‘Norchip’ and ‘Viking’ emergence still reduced potato yield by 15 to 25% (Nelson and Thoreson 1981). In other research, removing summer annuals by 20-cm potato height can prevent yield loss (Ciuberkis et al. 2007), and cultivation plus herbicide application at 60% predicted weed emergence resulted in greater yield than at 30% predicted emergence (Felix et al. 2009). If weed emergence is delayed by compost application, weed control may be reduced if cultivation is too early. Additionally, delaying cultivation after the 20-cm height to achieve 60% weed emergence may increase the risk crop injury.

Adding compost increases soil organic matter and soil enzyme activity, which could potentially increase weed-suppressive bacterial and fungal populations (Kremer and Li 2003). Researchers have suggested soil carbon may influence the amount of microbial activity (Davis et al. 2005), but later experiments that manipulated organic matter and available N did not affect giant foxtail seed decay (Davis 2007). Davis et al. (2006) observed a negative correlation between organic matter addition and soil fungal 18sRNA values, but Ullrich et al. (2011) observed no consistent relationship between microbial biomass and weed seed decay. These researchers mentioned that measurements of specific microbial functions, such as soil enzyme activity, may reveal a link between microbial activity and seed decay.

Extracellular soil enzyme activity may impact weed seed mortality by affecting the physical and chemical defense mechanisms of seeds. β -1,4-glucosidase (BG) is a soil enzyme involved in the degradation of cellulose in soil through hydrolysis of the disaccharide cellobiose into two separate glucose molecules (Muruganandam et al. 2009; Wernette 2011). β -1,4-N-acetyl glucosaminidase (NAG) is a soil enzyme that degrades chitin, and may degrade fungal

pathogens (Tronsmo and Harman 1993); however, NAG may affect beneficial fungi, such as arbuscular mycorrhizae. Both of these enzymes are thought to be positive soil health indicators (Muruganandam et al. 2009) and could contribute to rapid seed decay. Phenol oxidase (PHENOX) and peroxidase (PEROX) can degrade lignin (Sinsabaugh 2010), a component of weed seed coats. PEROX will depolymerize lignin, while PHENOX will oxidize the phenolic components. These soil enzymes may degrade phenolic weed seed defense components produced by seeds as secondary defense mechanisms (e.g., Davis et al. 2008; Kremer 1993; Mohamed-Yasseen et al. 1994). In addition, seed survival is related to seed coat thickness and hardness which are dependent on the cellulose, hemicellulose, and lignin content of the seed coat (Davis et al. 2008; Kremer et al. 1984; Mullin and Xu 2001; Rodgerson 1998). If soil enzyme activity increases because of compost application, degradation of secondary metabolites and weed seed coats may increase seed mortality. Seeds may be more vulnerable to decay or predation, or may be more apt to germinate if dormancy restrictions are lessened. Therefore, the objectives of this study were to investigate the impact of cured dairy manure compost on initial weed seed viability and innate dormancy, and to determine the effect of compost on weed seed mortality and dormancy and soil enzymatic activity in the year following compost application.

Materials and Methods

A field seed burial experiment was established in 2010 and repeated in 2011 at the Michigan State University Montcalm Research Center in Lakeview, MI. This study was conducted as a split-plot completely random design. The whole-plots were three rates of cured dairy manure compost at 0, 4, or 8 t carbon (C) ha⁻¹. The sub-plots were buried seeds of three weed species [common lambsquarters (CHEAL), giant foxtail (SETFA), hairy nightshade

(SOLSA) berries, and SOLSA seeds] from the three maternal environments of no, low, and high compost (N, L, and H, respectively). The soil was a mixture of Montcalm loamy sand and sandy loam (coarse-loamy, mixed, semiactive, frigid Alfic Haplorthods) and McBride loamy sand and sandy loam (coarse-loamy, mixed, semiactive, frigid Alfic Fragiorthods) with a pH 6.9 and 1.1% organic matter in 2010 and a pH 6.7 and 1.1% organic matter in 2011. The dates of all management practices are listed in Table 4.1.

Table 4.1. Schedule of various activities in the field.^a

Event	Time of Implementation	
	2010 – 2011	2011 – 2012
Fall tillage ^b	October 8 2009	October 8 2010
Spring tillage ^c	April 29	May 4
Compost and K fertilizer application	April 29	May 4
Potato planting	May 17	May 20
Preemergence herbicide application	May 19	May 20
Potato cracking and weed transplant (0 DAC)	June 7	June 7
Potato cultivation and N application	June 15	June 15
Potato hilling and N application	June 24	June 27
Topdress N application at canopy closure	July 7	July 7
End-of-season weed harvest	September 9	September 6
Seed bed tillage (disc to 10 cm depth)	October 8	October 15
Seed burial initiation	October 20 2010	October 22 2011
Enzyme and moisture measurements	- April 14 2011 May 20 June 15 July 19	March 27 2012
Seed burial termination	July 29	

^a Abbreviations: K, potassium; DAC, days after cracking; N, nitrogen.

^b Fall tillage consisted of using a disc in 2009 and a chisel plow in 2010.

^c Spring tillage consisted of using a disc in 2010 and using a disc followed by a field cultivator in 2011.

Weed Establishment. In the spring of each year, cured composted dairy manure¹ was applied by hand to 6.1 x 3.4 m plots and incorporated to 10 cm using a disc. A full analysis of the

compost in both years is listed in Table 4.2. Potatoes were planted (cut seed, approximately 42 to 47 g; ‘Snowden’ cultivar) mid-May each year (Table 4.1) using a two-row planter. Potatoes were planted in 0.86 m rows with 27 cm seed spacing at 10 cm depth. Nitrogen was balanced based on total inorganic nitrogen (N) application from the compost and inorganic fertilizer (LaMondia et al. 1999; Nyiraneza and Snapp 2007; Po et al. 2009), and was applied in four applications (30, 30, 20, and 20% at each timing, respectively). Table 4.3 summarizes initial soil test values and total macronutrient application in 2010 and 2011.

Table 4.2. Initial compost nutrient test from each year.^{a,b}

Soil Property	2010	2011
pH	9.3	8.6
Organic Matter	55.7%	49.5%
Carbon Content	32.3%	28.7%
Water Holding Capacity	-	15.0%
	ppm	
Total N	22600	20000
Inorganic-N (Ammonium-N/Nitrate-N)	-	27/381
P	5200	7200
K	19300	23100
Mg	11300	16900
Ca	43600	57700
S	3200	4600
B	26	37
Cu	71	102
Mn	291	312
Zn	137	212
Fe	3056	3195

^a Abbreviations: C, carbon; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; S, sulfur; B, boron; Cu, copper; Mn, manganese; Zn, zinc; Fe, iron.

^b Compost measurements containing a dash were not measured.

To establish a constant density of the three weed species, natural weed populations were controlled after potato planting using $0.23 \text{ kg ai ha}^{-1}$ linuron² + $0.58 \text{ kg ai ha}^{-1}$ S-metolachlor³ applied with a six-nozzle (50 cm spacing) carbon dioxide backpack sprayer at 190 L ha^{-1} and 330 kPa with TeeJet® XR8003 nozzles⁴ 45 cm above the soil surface. Weed transplants were

Table 4.3. Initial and applied macronutrient amounts in 2010 and 2011 by compost rate.^{a,b}

Nutrient	Initial soil levels (May)		0 t C ha ⁻¹		4 t C ha ⁻¹		8 t C ha ⁻¹	
Year	<u>2010</u>	<u>2011</u>	<u>2010</u>	<u>2011</u>	<u>2010</u>	<u>2011</u>	<u>2010</u>	<u>2011</u>
	mg kg ⁻¹							
Inorganic-N	-	6.2	116	121	116	118	115	115
P	200	224	4	4	27	34	50	64
K	182	142	17	17	103	114	206	228
Ca	483	401	0	0	258	317	517	635
Mg	88	77	5	5	67	93	134	186
S	12	9	21	21	19	25	38	51

^a Abbreviations: C, carbon; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; S, sulfur.

^b Soil and compost measurements containing a dash were not measured.

established in the greenhouse at Michigan State University in East Lansing, MI 4 wk prior to transplanting at the field site. Natural light was supplemented with artificial light for 16 hr per day at 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux to approximate summer light intensity and photoperiod during transplant production. Conditions in the greenhouse were maintained at day/night temperatures of 27/24 °C. Field collected seed for CHEAL⁵, SETFA⁶, and SOLSA⁷ were stored at 22°C for 24 hr, and SOLSA seeds were submersed in 2000 ppm gibberellic acid to stimulate germination (Spicer and Dionne 1961; Edmonds 1986). Four to 10 seeds of each species were planted into 25 x 40 mm media plugs⁸, and were thinned weekly to maintain a density of one plant per plug.

A single species was transplanted into the second and third row of each plot (with the exception of the weed-free plots) at potato cracking (Table 4.1). CHEAL and SOLSA were 2.5 cm tall at the time of transplanting, and SETFA was 7.5 cm tall, similar to Hutchinson et al. (2011). Weeds were transplanted into the row at a density of five plants per m row to simulate

weed emergence prior to potato emergence. Weed survival was evaluated 7 days after cracking (DAC) and weeds were thinned as needed to maintain plant density.

Irrigation was applied with a single-gun lateral system⁹ to the field as needed to supplement natural rainfall (Table 4.4). Rainfall and growing degree day accumulation (base 4°C) were recorded using the Michigan State University Enviro-weather station in Entrican, MI (Table 4.4). Fungicides and insecticides were applied to alleviate pest pressure when necessary based on weekly scouting reports.

Table 4.4. Growing degree day (GDD) accumulation (base 4°C), and rainfall and irrigation summary by month.

Month	2010 – 2011				2011 – 2012			
	GDD	Rainfall	Irrigation	Total	GDD	Rainfall	Irrigation	Total
		cm				cm		
April	358.0	3.8	0.0	3.8	182.1	8.6	0.0	8.6
May	610.4	9.1	0.0	9.1	566.8	7.9	0.0	7.9
June	800.8	7.9	0.0	7.9	787.0	6.1	0.0	6.1
July	1013.1	3.6	10.4	14.0	1033.9	4.3	10.2	14.5
August	978.2	4.9	5.3	10.2	882.4	6.6	2.8	9.4
September	576.7	4.6	0.0	4.6	578.0	6.1	0.0	6.1
October	342.2	3.8	–	3.8	343.2	4.1	–	4.1
November	104.0	2.5	–	2.5	140.0	3.3	–	3.3
December	4.6	0.8	–	0.8	17.1	2.3	–	2.3
January	–	–	–	–	–	–	–	–
February	–	–	–	–	–	–	–	–
March	–	–	–	–	337.9	5.6	–	5.6
April	182.6	8.6	–	8.6			–	
May	566.8	7.9	–	7.9			–	
June	787.0	6.1	–	6.1			–	
July	1033.9	4.3	–	4.3			–	
Total	7358.3	67.9	15.7	83.6				

Testing for Weed Seed Initial Viability and Dormancy. Weed seeds were collected from weeds in each plot at the end of the season (94 DAC in 2010 and 91 DAC in 2011). Seeds were separated by species and by compost rate (maternal environment). SOLSA seeds were manually

extracted from berries, and mature seeds were used for initial viability and dormancy testing. CHEAL and SETFA seeds were sieved (2.00, 0.85, and 0.50 mm) and passed through an air-column separator to remove excess chaff and immature seeds. Initial viability of mature seeds was assessed by cutting 100 seeds, placing them onto #2 Whatman filter paper in petri dishes, and soaking them in 15 *mM* triphenyl tetrazolium chloride (TTC). Viability was calculated by dividing the number of viable seeds by the total number of seeds tested. Innate seed dormancy was evaluated by placing 20 seeds on filter paper in petri dishes, wetting with deionized water, and dark germinating for 7 days. Percent dormancy (*d*) was calculated by using Equation [1]:

$$d = 100 * \left(1 - \left(\left(\frac{g}{n_1} \right) * \left(\frac{n_2}{v} \right) \right) \right) \quad [1]$$

where *g* is the number of seeds that germinated out of the number tested (*n*₁), and *v* is the number of viable seeds out of the number screened for viability (*n*₂).

Weed Seed Burial. After potato harvest, the field was tilled to 10 cm depth using a disc to prepare the seed bed for burial of seed bags (Table 4.1). Initial soil test values are listed in Table 4.5. Three seed bags [7 x 7 cm of 124 holes cm⁻² nylon mesh (Mitschunas et al. 2009)] containing 100 mature seeds of CHEAL, SETFA, SOLSA seed (in the berries), or SOLSA seed (extracted from the berries) from one maternal environment. To quantify the number of SOLSA seeds per berry, seeds were counted from 10 berries and averaged. Each bag was filled with unsieved soil from one weed-free plot area that received one level of compost the previous spring (0, 4, or 8 t C ha⁻¹). Bags without seeds were also buried to quantify native seed bank viability and induced dormancy. Seed bags were buried to 5 cm depth in October 2010 or 2011

(Table 4.1). The following April, soil samples (15 cm depth, 6 cores per plot) and volumetric water content¹⁰ (12 cm depth, ten readings per plot) was measured monthly (Table 4.6).

Table 4.5. Soil test values at the time of seed bag burial and harvest.^a

Soil Property	October 2010			July 2011			October 2011		
	0	4	8	0	4	8	0	4	8
	Compost rate (t C ha ⁻¹)								
pH	6.3	7.3	7.6	6.4	7.1	7.2	6.9	7.0	7.3
OM (%)	1.1	1.4	1.3	1.2	1.3	1.4	1.5	1.4	2.1
	ppm								
Inorganic-N	6.9/	13.8/	10.8/	9.6/	11.8/	13.9/	0.91/	0.91/	0.72/
(Ammonium-N/Nitrate-N)	5.0	4.0	2.1	1.6	2.0	2.6	0.53	0.25	0.29
P	171	180	219	129	153	171	172	177	200
K	126	231	338	78	127	209	107	203	222
Mg	64	108	148	80	111	126	107	103	123
Ca	394	662	786	426	476	568	474	530	634
S	15.0	13.0	15.0	9.0	8.0	8.0	10.0	8.0	12.0
B	0.2	0.3	0.6	0.1	0.2	0.3	0.2	0.2	0.3
Cu	3.4	3.6	3.5	10.2	9.5	9.5	3.8	4.0	2.7
Mn	15.5	21.4	22.5	9.4	16.3	17.2	11.8	9.4	14.2
Zn	2.0	3.4	3.6	3.2	4.0	3.9	2.2	1.8	2.7
Fe	43.6	53.3	53.0	48.7	55.6	60.0	41.3	34.9	40.1

^aAbbreviations: C, carbon; OM, organic matter; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; S, sulfur; B, boron; Cu, copper; Mn, manganese; Zn, zinc; Fe, iron.

Table 4.6. Volumetric water content (%) of the burial environments during the burial period.^{a,b}

Sampling Date	0 t C ha ⁻¹	4 t C ha ⁻¹	8 t C ha ⁻¹	LSD ^c (0.05)
4/14/11	8.35	7.69	7.77	n.s.
5/20/11	12.37	12.14	12.73	n.s.
6/15/11	7.39	6.71	7.14	n.s.
7/19/11	12.53	12.65	13.50	n.s.
7/29/11	15.44	16.62	18.89*	1.60
3/27/12	13.39	13.14	12.23	n.s.

^aAbbreviations: C, carbon.

^bAsterisk denotes significantly greater than the lowest value within a sampling date.

^cMeans within a row greater than the least significant difference (LSD) value are different from each other; n.s. indicates that treatments were not different from each other.

Testing for Seed Retention, Mortality, and Change in Dormancy. Seed bags were removed at the end of July and held at -18°C until September when seed bags were dried at 25°C for 48 h, and bag contents were passed through a series of four sieves (2.00, 0.85, 0.50, and 0.42 mm) for seed separation. Seed retention was calculated by dividing the recovered seed by the amount initially buried. Seeds that had emerged radicals were counted as fatally germinated, and seeds that were split were also separated. Ten recovered seeds were tested for viability by cutting seeds in half and placing the halves onto filter paper in petri dishes soaked with 15 mM TTC for 3 d. Viability was determined colorimetrically and was calculated by dividing the viable seed by the number tested. Seed mortality (μ) was calculated by Equation [2] from Schutte et al. (2008):

$$\mu = \frac{((s_0 + a_0) - (s_1 + g))}{(s_0 + a_0)} \quad [2]$$

where s_0 is the amount of seed initially buried, a_0 is the number of ambient seeds in the soil, s_1 is the viable seed after burial, and g is the number of seeds that fatally germinated. Twenty seeds were dark germinated on filter paper moistened with deionized water in petri dishes at 23°C for 7 d. To calculate seed dormancy after burial, the number of germinated seeds was divided by the number of seeds tested, multiplied by the inverse of the percent viable, and this value subtracted from one. To calculate the change in dormancy, the initial dormancy within a species and maternal environment was subtracted from the calculated dormancy after the burial period.

Soil Enzyme Activity. Soil enzyme activity was measured following the procedure outlined in Sinsabaugh et al. (2002). Samples were taken monthly (Table 4.1), and activity of β -1-4-glucosidase (BG), β -1-4-*N*-acetyl-glucosaminidase (NAG), phenol oxidase (PHENOX), and

peroxidase (PEROX) was quantified. Soil was kept at -18°C until processing. Soil was sieved (2.00 mm), and pH was determined. One gram of soil was homogenized with 125 mL of 50 mM sodium acetate buffer at the soil's pH for 1 min. Fluorimetric assays for BG and NAG were conducted in black trays, whereas the colorimetric assays for PHENOX and PEROX were conducted in clear microplates.

In each fluorescence tray had a total of 96 wells; 24 wells were used to establish standards, and 24 wells were used per soil sample. The standards consisted of eight control wells containing only 250 μL of 50 mM buffer, eight wells containing 200 μL buffer + 50 μL of fluorescence standard [10 μM 4-methylumbelliferone (4-MUB) for BG and NAG], and eight wells containing 200 μL buffer + 50 μL of substrate solution (200 μM 4-MUB glucoside for BG; 200 μM 4-MUB-*N*-acetyl- β -D-glucosaminide for NAG; 25 mM L-3,4-dihydroxyphenylalanine for PHENOX and PEROX). For each soil sample, 16 wells contained 200 μL soil extract + 50 μL of substrate solution, and eight wells contained 200 μL soil extract + 50 μL of fluorescence standard to measure fluorescence of the soil before substrate was added. No fluorescence standard was used in the colorimetric plates. In the PEROX assay, 10 μL of 0.3% hydrogen peroxide solution was added in addition to the 50 μL substrate solution. Assays were dark incubated at 15°C for 6 h, and reaction was terminated with 10 μL of 1.0 M sodium hydroxide. Fluorescence of BG and NAG was measured with a microplate fluorometer¹¹ using a 355 nm excitation and a 460 nm emission filter. Colorimetric assays of PHENOX and PEROX measured absorbance at 450 nm¹². All enzyme activity is reported in $\text{nmol h}^{-1} \text{g}^{-1}$.

Statistical Analysis. Data were analyzed using a one-way ANOVA with the MIXED procedure in SAS® 9.2¹³. Compost rate, weed species, maternal environment, and their interactions were treated as fixed factors, with year and replication as random factors. Normality of the residuals was evaluated by visual examination of normal probability and stem-and-leaf plots. Homogeneity of the variances was evaluated by residual plots, box plots, and Levene's test ($\alpha=0.1$) and grouped to reduce the AIC value of the model using the GROUP option of the REPEATED statement. When the year by factor interaction was not significant, data were combined across years. When the interaction between compost rate and weed species was found to be significant, comparisons between the combinations at each compost rate and weed species level were examined by slicing and conducting individual pair-wise comparisons using t-tests when slicing results were significant ($\alpha=0.05$). When factors were found to be significant ($P\leq 0.05$), all-pairwise comparisons were conducted using Fisher's protected LSD. The PROC CORR procedure was used in SAS to correlate seed mortality and dormancy to soil enzyme activity and water level in the soil at each sampling time. A significant correlation was present if $P\leq 0.05$, and the Pearson correlation coefficient (r) was reported.

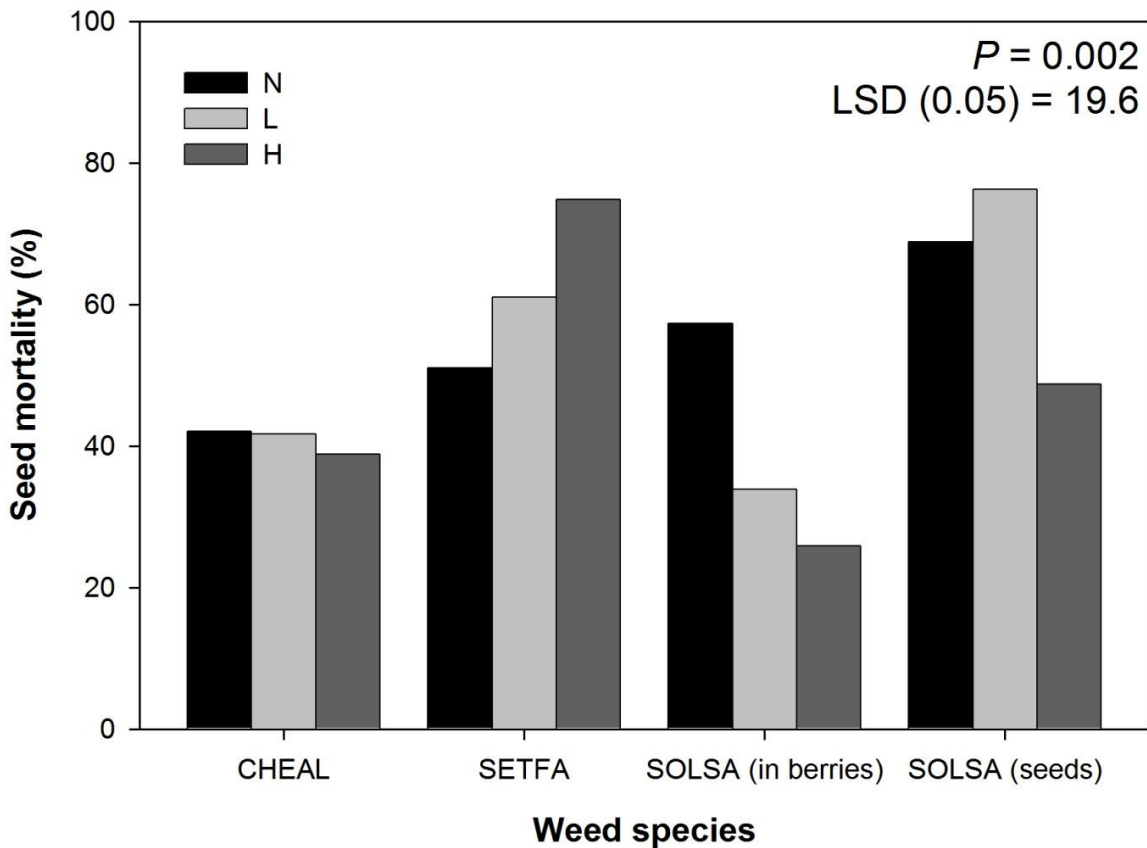
Results and Discussion

Maternal Environment Effects on Weed Seed Mortality and Dormancy. There was no effect of compost on weed fecundity or the number of mature seeds produced per gram dry biomass (Lindsey et al. 2011). Furthermore, maternal environment (compost rate) had no effect on initial viability or innate dormancy of seeds of any weed species. Across environments and years, initial viability of CHEAL, SETFA, and SOLSA was 97, 58, and 98%, respectively; innate dormancy was 76, 79, and 99%, respectively. The initial viability values differed for Forcella et al. (1996)

in Minnesota, who observed initial viability of 79 and 48% for green foxtail and CHEAL, respectively, but growing degree day accumulation (10°C base) in Minnesota was less than in Michigan (500 to 1000 fewer GDD) and may have reduced initial viability of CHEAL. Native CHEAL seed was present in the unsieved soil used to fill the seed bags; the adjusted viability and dormancy of the buried CHEAL seed was 66 and 97%, respectively. In this seed burial study, the maternal temperature and soil moisture environments were similar across compost treatments because of irrigation, and nitrogen was balanced across compost treatments. Therefore, it was not unexpected to observe similar values of innate seed dormancy because of maternal environment (Fenner 1991).

No difference in seed retention was observed because of maternal environment. Retention of CHEAL, SETFA, SOLSA seeds in berries, and SOLSA seeds alone was 88, 72, 99, and 71%, respectively, averaged across maternal and burial environments. However, seed mortality was influenced by maternal environment (Figure 4.1). SOLSA seed in berries had the least seed mortality, particularly when plants were grown under compost, but SOLSA seed alone had greater seed mortality. SETFA seed from composted treatments experienced the greatest seed mortality. In previous studies, SETFA seed mortality was greater than CHEAL and velvetleaf seed mortality (e.g., Davis et al. 2005; Schutte et al. 2008). The effects of maternal environment on seed viability may be a result of seed coat formation and composition. Davis et al. (2008) quantified phenolics in the seed coat and observed greater phenolic concentrations in SETFA seeds compared to CHEAL. However, as seed coat thickness increased phenolic compound concentration decreased, indicating SETFA may be more reliant on defense compounds as compared to physical seed protection. In a separate seed study by Schroeder et al. (1974) that examined physical properties of seeds, the seed fiber content of CHEAL, green foxtail, and black

Figure 4.1. Weed seed mortality as affected by maternal environment. N is the maternal environment that had no compost applied, L is where 4 t carbon (C) ha⁻¹ was applied, and H is the maternal environment that received 8 t C ha⁻¹. Means greater than the least significant difference (LSD) value are different from each other ($P=0.002$). Common lambsquarters (CHEAL) mortality was unchanged over the 9 month burial period. Giant foxtail (SETFA) mortality increased, and hairy nightshade (SOLSA) mortality decreased as the compost in the maternal environment increased.



nightshade was 15.1, 12.4, and 40.3%, respectively. When soil is amended with compost, seed coat properties such as lignin content and phenolic compound concentration may change and influence weed seed mortality.

Across all environments, SETFA dormancy increased during the nine months of burial by 30%, CHEAL dormancy decreased by 5%, and SOLSA dormancy was unchanged (Table 4.7). Both SETFA and CHEAL dormancy after burial were significantly different than dormancy at the time of burial. This suggests a portion of the CHEAL seed persisting through the burial

period shifted from an innate dormancy to an enforced dormancy (Fenner 1985). In addition, many SETFA seeds fatally germinated, resulting in the remaining seed exhibiting greater levels of innate, enforced, or induced dormancy.

Table 4.7. Change in weed seed dormancy after the burial period for common lambsquarters, giant foxtail, hairy nightshade seeds buried in berries, and hairy nightshade seeds alone from each maternal environment.^a

Species	Maternal environment			Mean ^b
	N	L	H	
	%			
CHEAL	-4.97	-3.36	-7.67	-5.33c
SETFA	34.63	13.24	41.30	29.72a
SOLSA (in berries)	1.80	1.80	-1.53	0.69b
SOLSA (seeds alone)	1.48	0.87	-1.90	0.15b

^a Abbreviations: N, no compost applied; L, low compost applied; H, high compost applied; CHEAL, common lambsquarters; SETFA, giant foxtail; SOLSA, hairy nightshade.

^b Average is for within a species only. Letters denote differences in seed production between species averaged across maternal environments ($P < 0.001$). Interaction of maternal environment and species was not significant.

SOLSA dormancy may have remained unchanged because of greater primary dormancy mechanisms (Taab and Andersson 2009) such as physical restrictions because of greater fiber content or metabolic triggers. Great variability exists in the temperature, moisture, and pH requirements to break dormancy (Zhou et al. 2005a), and additional studies demonstrate exposure to potassium nitrate or gibberellic acid is necessary to break dormancy of Solanaceae species (Bithell et al. 2002; Spicer and Dionne 1961; Zhou et al. 2005b). Schroeder et al. (1974) reported 34-40% of the seed was fiber in members of the Solonaceae family, whereas fiber content in the seed of foxtails and CHEAL was below 16%. These properties may all contribute to the high level of dormancy observed in SOLSA seeds.

Effect of Burial Environment on Weed Seed Retention, Mortality, and Dormancy. Seed retention was not influenced by burial environment. Seed retention was 86, 79, and 83% for the

0, 4, and 8 t C ha⁻¹ burial environments, respectively, when averaged over weed species. Seed mortality was also not influenced by burial environment, but minor increases in seed decay were observed for CHEAL, SETFA, and SOLSA seed in berries as compost in the burial environment increased (Figure 4.2).

Figure 4.2. Weed seed mortality (a and b) of common lambsquarters (CHEAL), giant foxtail (SETFA), hairy nightshade (SOLSA) seeds buried in berries, and hairy nightshade seeds alone was not significantly affected by burial environment (t carbon (C) ha⁻¹).

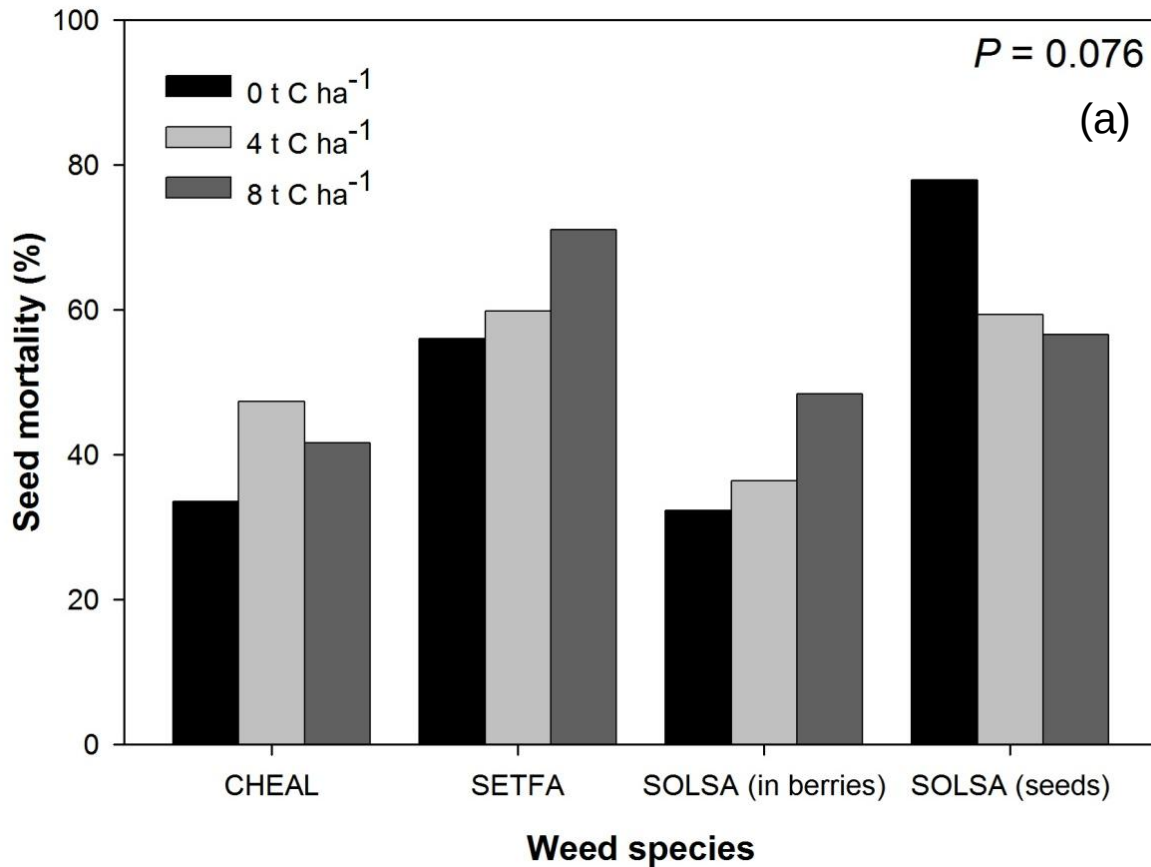
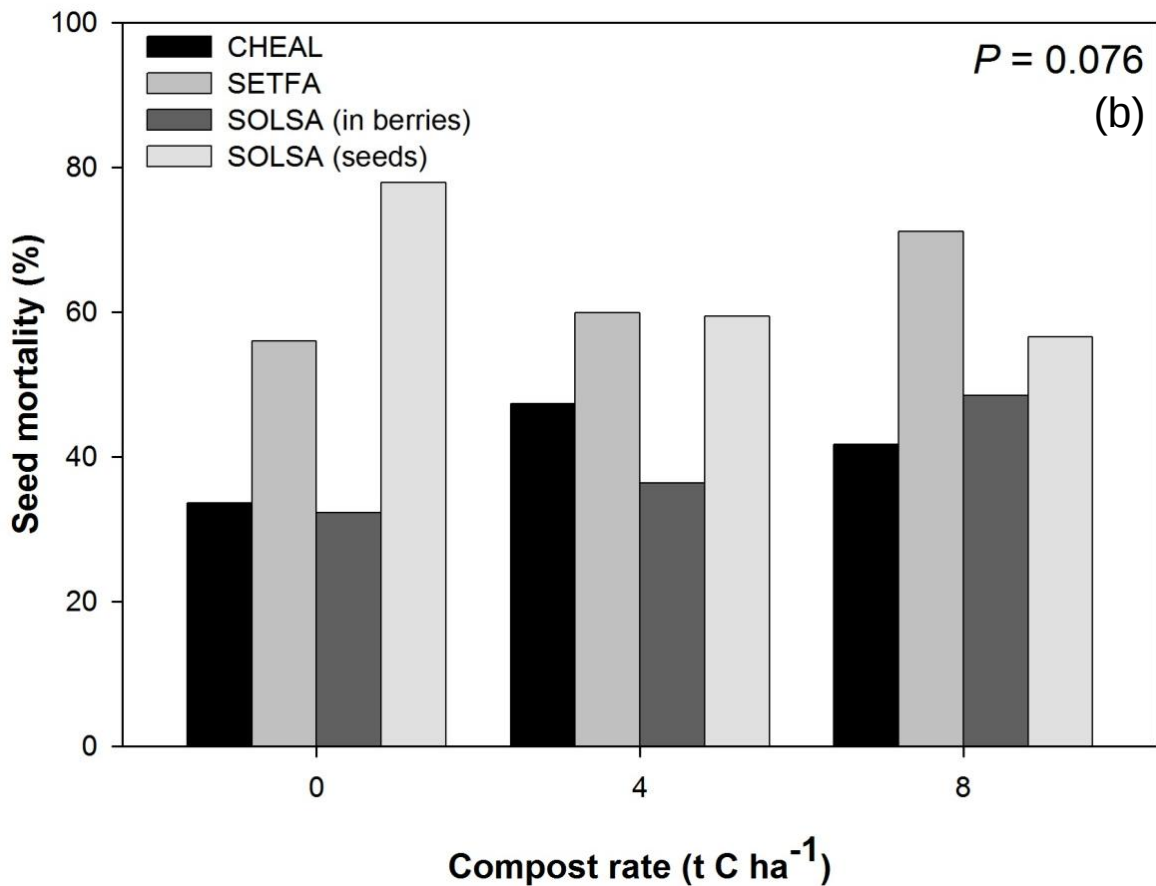


Figure 4.2 (cont'd).



In addition, the change in dormancy was not influenced by burial environment. Schutte et al. (2008) observed an effect of burial environment on mortality of SETFA and velvetleaf seed that they attributed to differences in soil moisture at two separate burial sites. In our study, volumetric water content in the soil was similar across compost rates at all sampling dates with the exception of harvest in 2011 (Table 4.6) and was not correlated to mortality of any species. Research by Schutte et al. (2008) suggests maternal environment as more influential on seed survival compared to burial environment, supporting our results. Differences also may have been less apparent in a single year of burial, whereas annual compost applications in a five-year experiment reduced the weed seed-bank compared to the treatment receiving only mineral N fertilization (De Cauwer et al. 2009). Applying 45 t ha⁻¹ beef cattle manure and 22 t ha⁻¹ cull

potato compost for five consecutive years reduced weed seed-bank values when tillage was used to control weeds, but when herbicides were used seed-bank values were unchanged (Gallandt et al. 1998).

Burial Environment Effects on Soil Enzyme Activity. The soil pH at all timings was between 6.7 and 7.3, and soil enzyme assays were conducted near neutral pH. Soil enzyme activity of BG (responsible for cellulose depolymerization) was greater at most timings when compost was applied (Figure 4.3 a-e). Activity of NAG (responsible for chitin depolymerization) exhibited a similar pattern. These indicators increased under compost, and may suggest a healthier soil microbial population (Muruganandam et al. 2009). Activity of BG was strongly correlated with NAG ($r=0.614$, $P<0.001$), which may be because BG is produced by fungi (Lammirato et al. 2010), and NAG activity is positively correlated with fungal activity (Muruganandam et al. 2009). A negative correlation was present between NAG and volumetric water content ($r=-0.29$, $P<0.001$), suggesting as soil moisture decreased fungal activity increased. Lower soil moisture may have allowed for better aeration causing an increase in fungal populations (Griffin 1963). Only SOLSA seed mortality was negatively correlated with NAG activity ($r=-0.19$, $P=0.028$); however, this correlation may not have been biologically significant.

PEROX activity (responsible for degrading lignin) was only greater in amended soils than the non-amended at the May timing after 8 t C ha⁻¹ compost was applied (Figure 4.4 a-e). PHENOX activity, an enzyme responsible for degrading phenolic compounds, varied by timing and was greater in May, June, and July when 8, 4, or 8 t C ha⁻¹ was applied, respectively (Figure 4.4 b, c, and d). Lignin degrading enzyme activity was the greatest when no compost was applied. PHENOX was negatively correlated with BG activity ($r=-0.241$, $P=0.005$) and PEROX

Figure 4.3 (a-e). β -1,4-glucosidase (BG) and β -1,4-*N*-acetyl glucosaminidase (NAG) soil enzyme activity over time. Letters denote differences in burial environment within an enzyme and sampling date, and *NS denotes no difference. Bars depict one standard error of the mean.

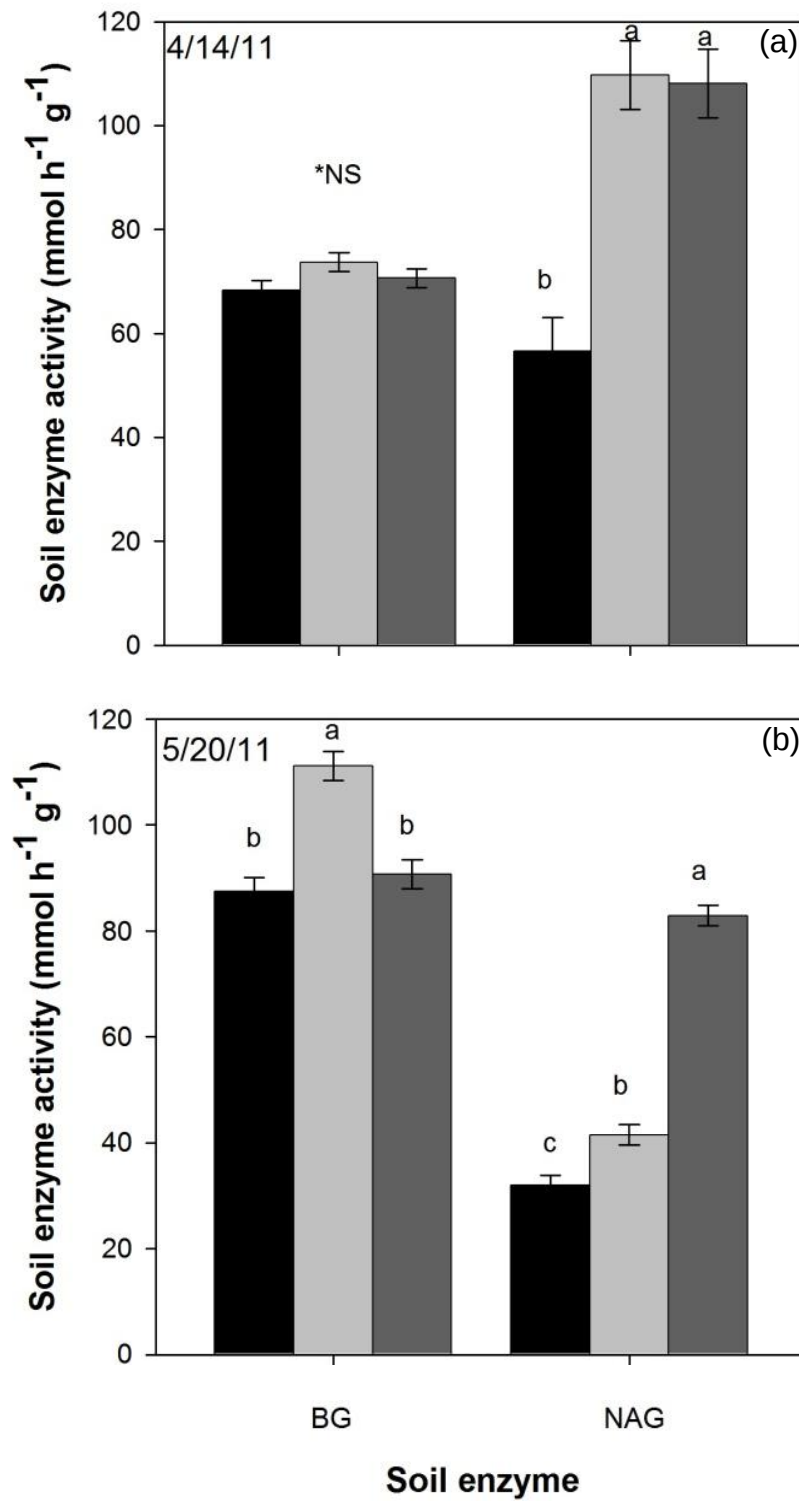


Figure 4.3 (cont'd).

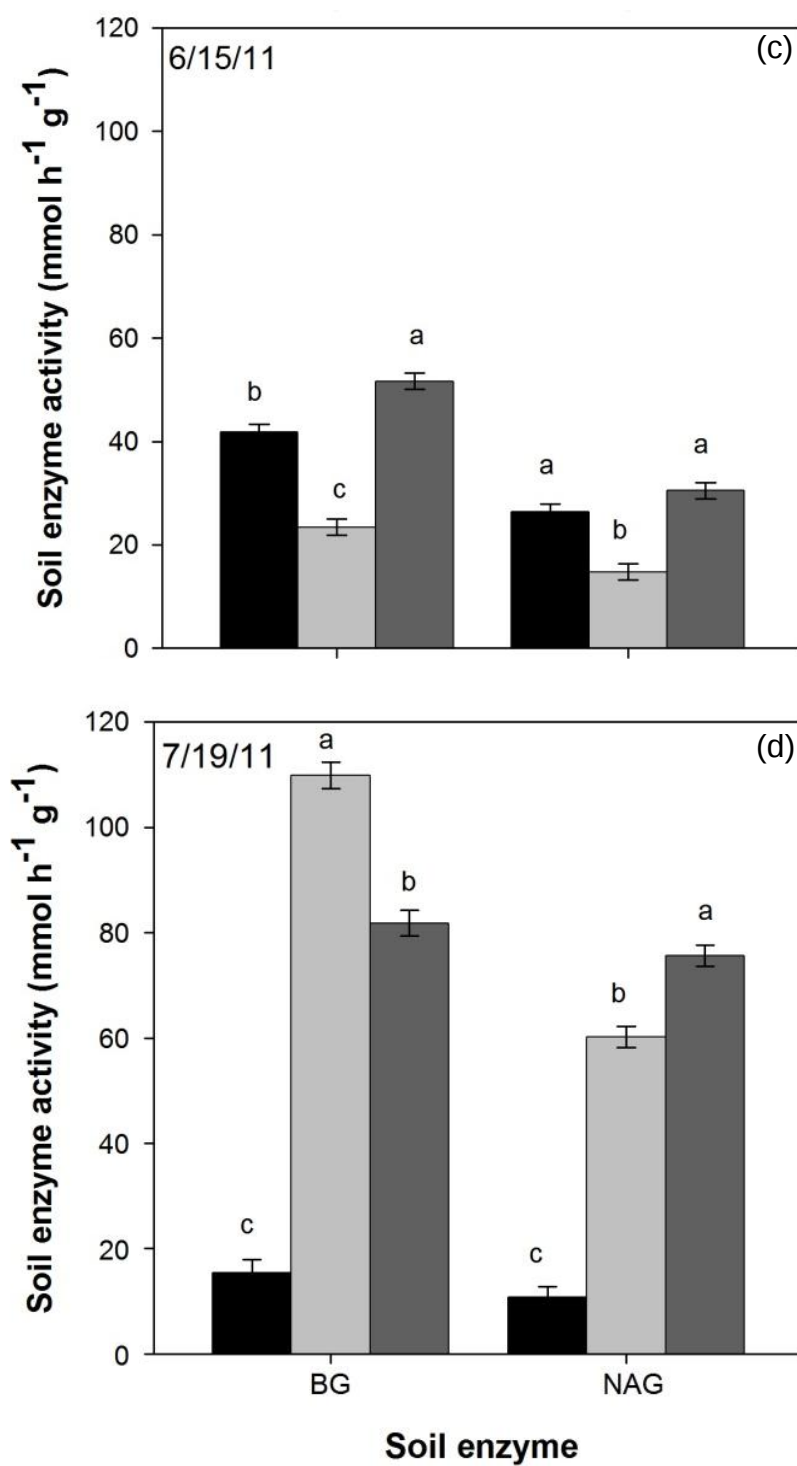


Figure 4.3 (cont'd).

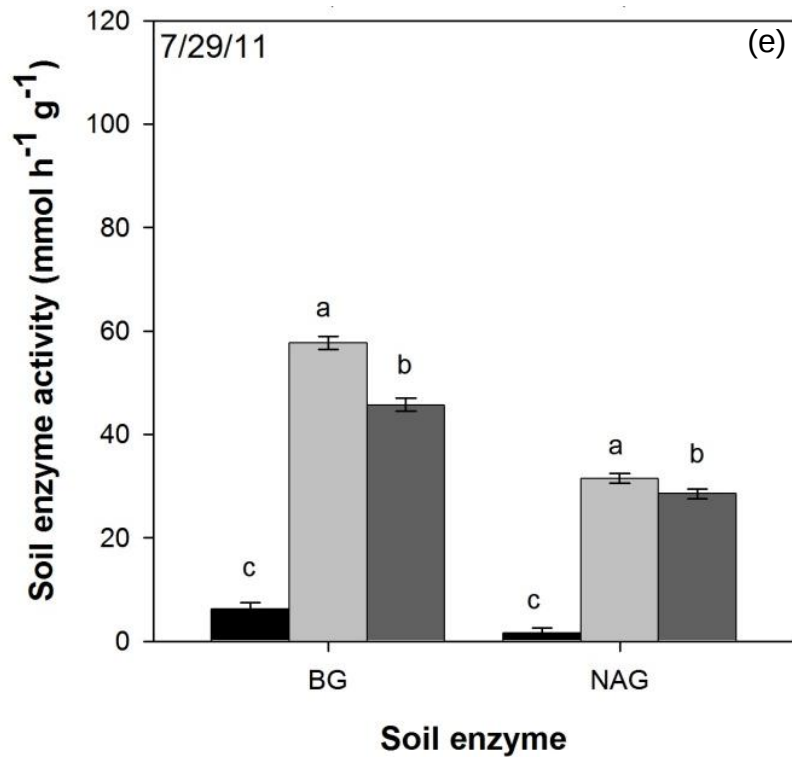


Figure 4.4 (a-e). Phenol oxidase (PHENOX) and peroxidase (PEROX) activity over time. Letters denote differences in burial environment within an enzyme and sampling date. Bars depict one standard error of the mean.

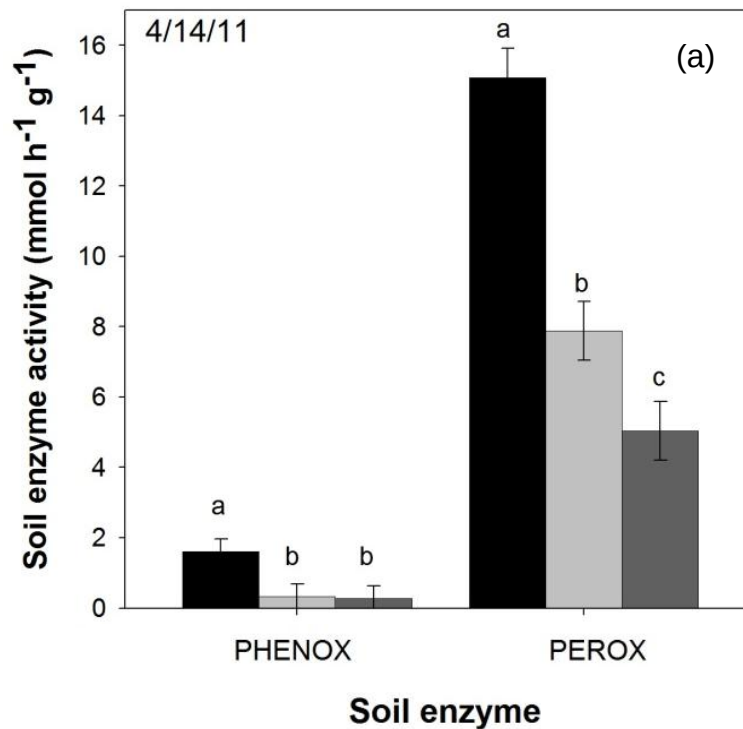


Figure 4.4 (cont'd).

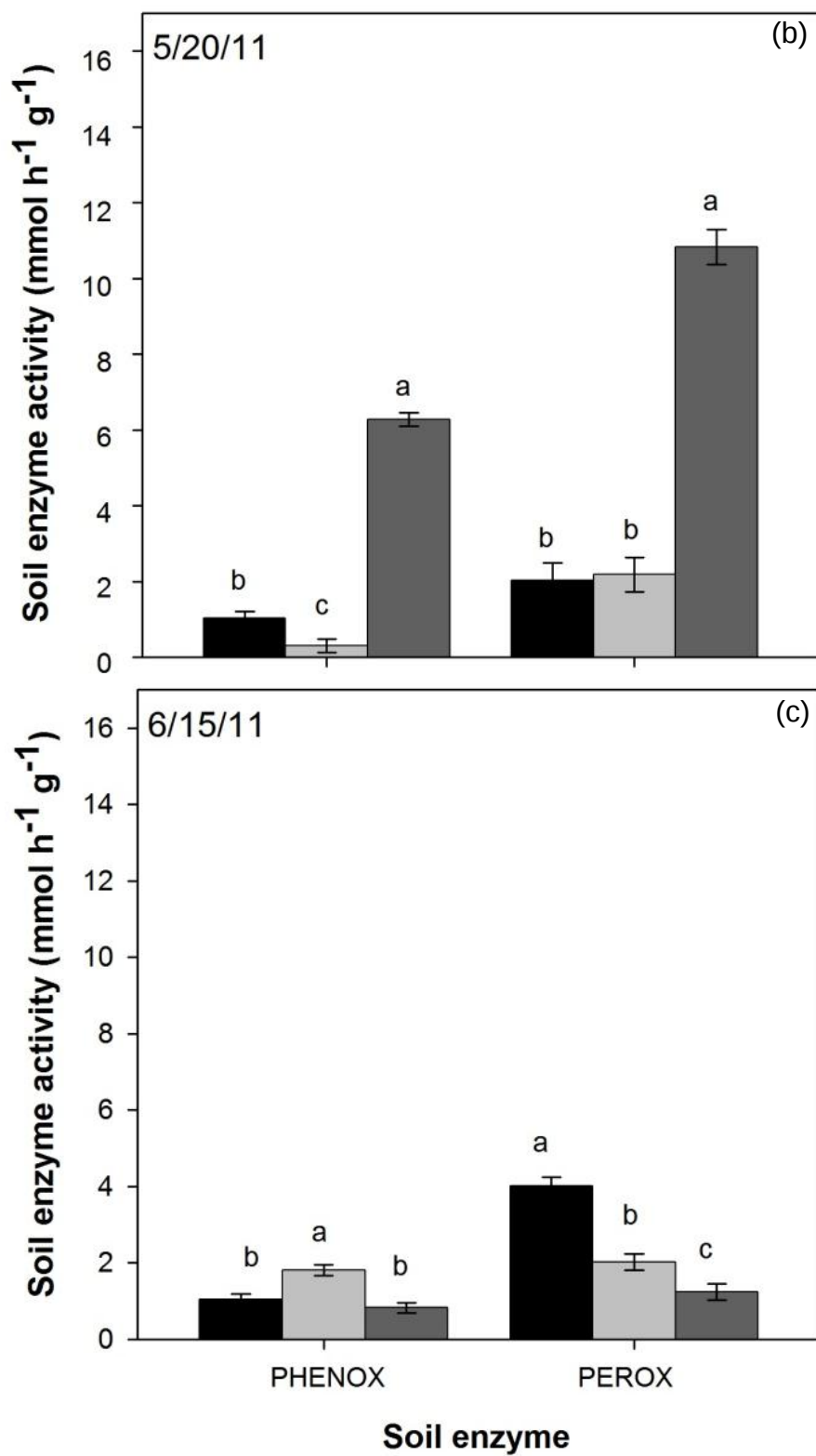
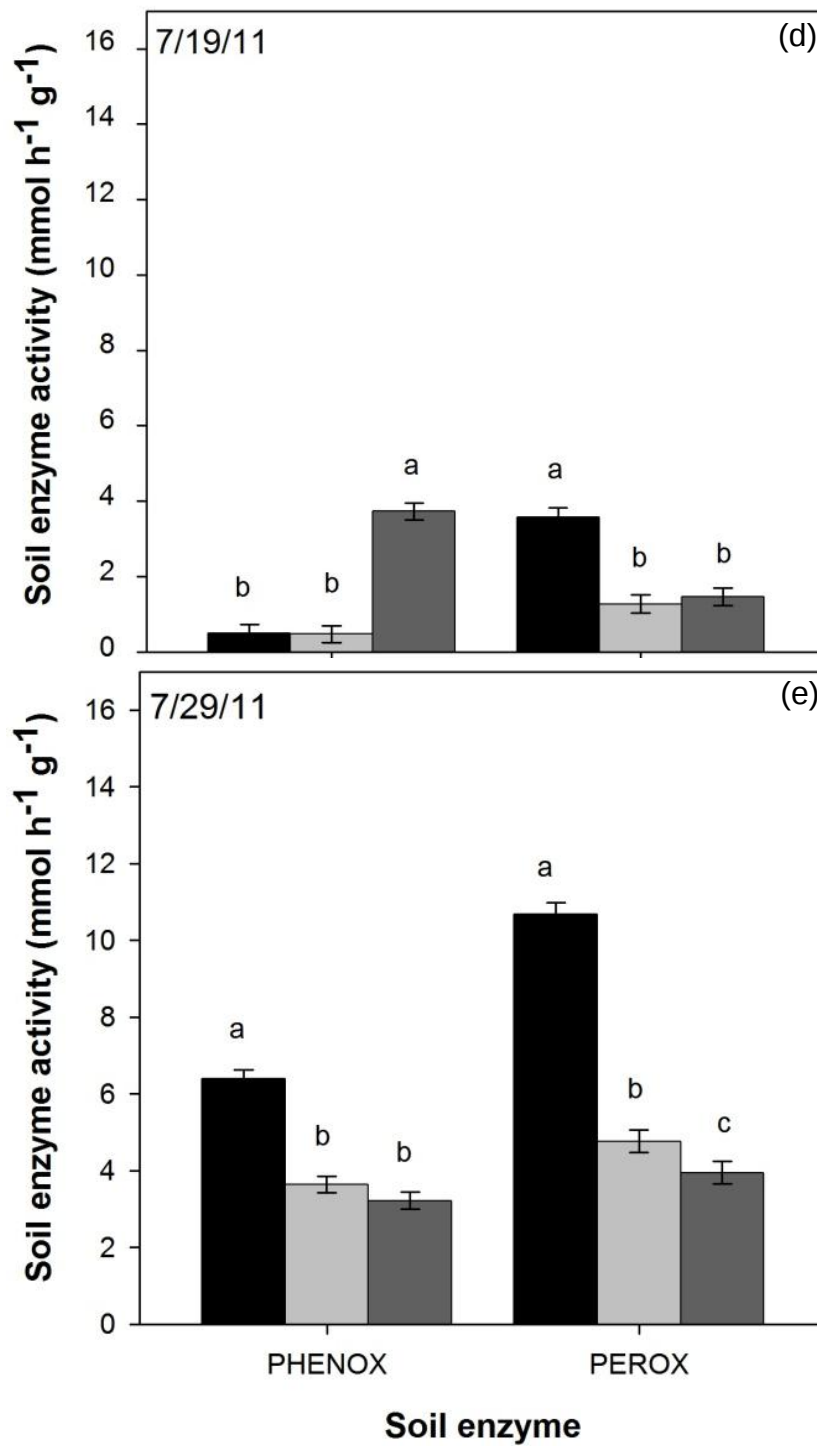


Figure 4.4 (cont'd).



activity was correlated with NAG ($r=0.198$, $P=0.0213$), which may suggest enzyme regulation; as enzymes that degrade cellulose decrease in activity, lignin degrading enzyme activity

increases. PHENOX and PEROX activity experienced a positive correlation ($r=0.445$, $P<0.001$), which may be because both these enzymes are involved in lignin degradation. Lignin degradation requires activity of both PEROX and PHENOX, with PEROX degradation occurring first. Therefore, soils receiving no compost may be able to degrade lignified tissue at a faster rate than amended soils. If secondary phenolic defense compounds were in the seed coat or were contained in berry exudates, it would be expected these compounds would more readily be metabolized where compost was applied by the PHENOX enzymes because elevated activity was observed in three of five sampling dates. Dormancy of the weeds may also be influenced by PHENOX if it degrades the phenolic compounds in the seed coat that regulate germination by absorbing oxygen to prevent the seed embryo from germinating (Baskin and Baskin 1998).

Davis et al. (2008) quantified various secondary defense compounds, and measured greater production in SETFA than in CHEAL seeds. Therefore where compost was applied seed mortality of SETFA would be greater than CHEAL, which was observed in this study but was not statistically significant. Few differences in seed retention and mortality between burial environments indicate soil enzymes were not degrading weed seed coats with observable results. Increases in microbial biomass with organic management versus conventional management did not increase weed seed persistence in previous research (Ullrich et al. 2011), suggesting other factors may be more important in weed seed decay than the burial environment (Schutte et al. 2008). Differences in species survival may indicate differences in defense mechanisms that were species specific and influenced by maternal environment. In soybeans, complex carbohydrate content (hemicelluloses) was correlated to seed hardness and water uptake (Mullin and Xu 2001), which could influence the longevity of seed viability.

In conclusion, compost does not affect weed seed production but may influence seed survival. In addition, the maternal environment effects on seed survival may be more important than the burial environment. Decreased mortality of weed seeds because of maternal environment may increase weed infestations and introduce new weeds to fields if tillage equipment is not cleaned. Differences in seed coat composition and defense compounds may help explain differences observed in seed viability, and should be examined in future studies.

Sources of Material

- ¹ University Farms, Michigan State University, East Lansing, MI 48824.
- ² Lorox®, Tessenderlo Kerley, Inc, 55 N. 44th Street, Suite 300, Phoenix, AZ 85008.
- ³ Dual II Magnum®, Syngenta Crop Protection, Inc, P.O. Box 18300, Greensboro, NC 27409.
- ⁴ TeeJet® Technologies, 1801 Business Park Drive, Springfield, IL 62703.
- ⁵ Agronomy Farm - October 2006, East Lansing, MI 48824.
- ⁶ Agronomy Farm - October 2007, East Lansing, MI 48824.
- ⁷ Field Collected - October 2009, Lakeview, MI 48854.
- ⁸ 25mm Ellepot in Blackmore 105/27 Ellepot tray, Ellepot USA/Blackmore Company, Inc, Belleview, MI 48111.
- ⁹ Reinke Single-Gun Lateral Irrigator, Reinke Manufacturing Company, Inc, 5325 Reinke Road, Deshler, NE 68340.

- ¹⁰ FieldScout TDR 300 Soil Moisture Meter, Spectrum Technologies, Inc, 12360 South Industrial Drive East, Plainfield, IL 60585.
- ¹¹ Fluoroskan II, Thermo Labsystems, Waltham, MA.
- ¹² Spectranmax Microplate Spectrophotometer, Molecular Devices Inc. Sunnyvale, CA.
- ¹³ SAS® 9.2 Software, SAS Institute Inc, 100 SAS Campus Drive, Cary, NC 27513.

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