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Hanna J. Poffenbarger, Steven B. Mirsky, John R. Teasdale, John T. Spargo, Michel A. Cavigelli, and Matthew Kramer*

Crop yields can be similar in organic and conventional systems even when weed biomass is greater in organic systems. Greater weed tolerance in organic systems may be due to differences in management-driven soil fertility properties. The goal of this experiment was to determine whether soil collected from a long-term organic cropping system with a diverse crop rotation and organic fertility inputs would support higher soil nitrogen (N) resource partitioning, as indicated by overyielding of corn–weed mixtures, than a cropping system with a less diverse crop rotation and inorganic N inputs. A replacement series greenhouse experiment was conducted using corn : smooth pigweed and corn : giant foxtail proportions of 0 : 1, 0.25 : 0.75, 0.5 : 0.5, 0.75 : 0.25, and 1 : 0 and harvested at 29, 40, or 48 d after experiment initiation (DAI). The monoculture density of corn was 4 plants pot^{-1} and the monoculture density of each weed species was 36 plants pot^{-1}. Corn was consistently more competitive than both weed species at 40 and 48 DAI when soil inorganic N was limiting to growth. Corn–smooth pigweed mixtures had greater shoot biomass and shoot N content than expected based on the shoot biomass and shoot N content of monocultures (i.e., overyielding) at the onset of soil inorganic N limitation, providing some evidence for N resource partitioning. However, soil management effects on overyielding were infrequent and inconsistent among harvest dates and corn–weed mixtures, leading us to conclude that management-driven soil fertility properties did not affect corn–weed N resource partitioning during the early stages of corn growth.
Nomenclature: Giant foxtail, *Setaria faberi* Herrm. SETFA; smooth pigweed, *Amaranthus hybridus* L. AMACH; corn, *Zea mays* L.
Key words: De Wit replacement series, overyielding, resource partitioning.

Crop yield or quality losses due to weeds continue to challenge farmers, particularly those attempting to reduce external inputs or manage weeds using organic farming methods. In a recent survey of U.S. organic farmers, 50% of respondents reported that weeds were the primary constraint to crop production (Ryan et al. 2008). The most common approach to weed management is through direct control tactics such as herbicides and cultivation. However, concerns about environmental and health risks of agrochemical exposure, along with the ability of weed communities to shift in response to control practices, have prompted scientists to study integrative approaches to weed management that consider crop–weed competition dynamics and reduce reliance on external inputs (Buhler 2002; Davis et al. 2009; Mortensen et al. 2000; Wilson et al. 2009).

Competition has been defined by weed scientists as the struggle between a crop and a weed for a shared resource that is in short supply (Zimdahl 2004). One ecological approach to weed management involves reducing crop–weed competition by maximizing resource partitioning, which occurs when species differ in their means of acquiring limited resources (e.g., sunlight, water, nutrients, or space). Resource partitioning allows diverse plant communities to utilize a limited resource more efficiently than monocultures, leading to overyielding. Overyielding occurs when the productivity of a mixture exceeds expectations based on monoculture yields (Harper 1977). Some plant communities demonstrate resource partitioning for limited belowground resources such as N. For example, researchers have observed differentiation of rooting patterns over time and space in early successional

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plant communities (Jumpponen et al. 2002; McKane and Grigal 1990; Parrish and Bazzaz 1976). Furthermore, research suggests that individual plant species can preferentially use specific forms of inorganic N [corn: Teyker 1992; giant foxtail: Salas et al. 1997; and redroot pigweed (*Amaranthus retroflexus* L.): Teyker et al. 1991] and even organic N forms (albeit primarily in severely N-limited environments; Ashton et al. 2010; Bol et al. 2002; Harrison et al. 2007) to avoid competition. Plant communities comprising legumes and nonlegumes often demonstrate complementary N acquisition because legumes form a symbiotic relationship with N-fixing rhizobia, which allows them to obtain N from the atmosphere rather than the soil (Hauggaard-Nielsen et al. 2009; Jensen 1996).

Organic and conventional systems can produce similar corn and soybean [*Glycine max* (L.) Merr.] yields despite greater weed biomass in organic systems (Davis et al. 2005; Delate and Cambardella 2004; Ryan et al. 2009). To explain this finding, Smith et al. (2010) proposed a resource pool diversity hypothesis (RPDH), which posits that increased diversity of crops and organic amendments in a cropping system results in differentiated soil resource pools (in time, space, and chemical forms), which provide distinct niches for species that can draw soil resources from different pools. The hypothesis is congruent with studies that point to the importance of N quantity (Blackshaw et al. 2003; Blackshaw and Brandt 2008; Wortman et al. 2011), source (Blackshaw 2005; Davis and Liebman 2001; Dyck and Liebman 1994; Dyck et al. 1995), timing (Alkamper et al. 1979; Anderson 1991; Harbur and Owen 2004), and spatial location (Blackshaw et al. 2002; Melander et al. 2003) on the relative growth and N uptake of crops and weeds, and on crop–weed competition in agroecosystems.

Providing evidence for the RPDH, Smith et al. (2010) summarized results from several long-term studies that suggest that greater resource diversity in organic systems may buffer against crop yield loss in the presence of high weed biomass. A controlled crop–weed competition experiment in microplots at Rodale Farming Systems Trial also supported the RPDH by showing reduced corn yield loss per unit weed biomass in the organic vs. conventional system (Ryan et al. 2010). However, organic and conventional systems in long-term experiments are often characterized by several confounding factors that make the RPDH difficult to clearly test within field trials. For example, Ryan et al. (2010) suggested that system differences other than resource pool diversity, such as planting date and weed species differences, may have accounted for their findings. Additional confounding factors between organic and conventional systems could include crop cultivar, tillage, and crop density (Cavigelli et al. 2008). To explicitly test the RPDH, crop–weed competition must be assessed in a controlled study, with soil management legacy plus fertility source isolated as the independent variable.

The replacement series experimental design is one design particularly suited to assess crop–weed competition, plant community overyielding, and the potential for resource partitioning in soils from contrasting management systems. In the replacement series design, the total density of plants remains constant while the proportions of two species vary. There is a long-standing debate in plant ecology literature on the value of the replacement series experimental design due to the biases that can be introduced from differences in initial plant size or resource use of the two species and dependence of competition indices on total density selected. To address bias that results from differences in plant size or resource use among species with an equivalent number of individuals, Connolly et al. (2001) proposed the use of functional densities, which differ in the number of individuals but result in equivalent size or resource use (as measured by biomass, leaf area, shoot N content, etc.) of monocultures. Taylor and Aarssen (1989) noted that density dependence of competition indices may be minimized when demands on resources equal the supply (i.e., constant final yield). Constant final yield is also a requirement for overyielding to be accurately interpreted as resource partitioning (Sackville-Hamilton 1994; Taylor and Aarssen 1989).Therefore, the replacement series design, implemented correctly, requires careful manipulation of monoculture densities, resource availability, and experimental duration.

We implemented a controlled replacement series greenhouse experiment to determine whether soil collected from a long-term organic cropping system with a diverse crop rotation and organic fertility inputs would support higher N resource partitioning, as indicated by overyielding of corn–weed mixtures, than soil collected from a cropping system with a less diverse crop rotation and inorganic N inputs. Specifically, we wanted to determine (1) the effects of soil management on the relative competitiveness of corn and weeds; (2) if overyielding occurs in corn–weed mixtures, providing evidence for soil N resource partitioning; and (3) whether the extent of N resource partitioning is greater in organically than conventionally managed soils.

Materials and Methods

Experimental Design. A completely randomized replacement series experiment, which included corn competing with either smooth pigweed or giant foxtail in soil collected from an organic or conventional system, was conducted from August through October 2011 in a greenhouse at the Beltsville Agricultural Research Center in Beltsville, MD (39°54′N, 76°56′W). The experiment included three harvest dates to address possible temporal bias associated with sampling at a single time point (Connolly et al. 1990). Conducting the experiment in a greenhouse setting allowed us to limit N availability while maintaining sufficient supplies of light, water, and other soil nutrients. However, the use of pots in a greenhouse setting meant that competition could only be evaluated during the initial stages of corn growth due to the limited soil inorganic N supply that impeded plant growth after several weeks.

Corn and each weed species were grown at corn : weed proportions of 0 : 1, 0.25 : 0.75, 0.5 : 0.5, 0.75 : 0.25, and 1 : 0, where the monoculture density of corn was 4 plants pot^{-1} and the monoculture density of the weed (giant foxtail or smooth pigweed) was 36 plants pot^{-1}. The total densities selected for the greenhouse competition experiment (4 corn plants pot^{-1} and 36 weed plants pot^{-1}) represented equivalent N use and constant final N uptake based on a preliminary experiment, conducted June through August of 2011 using the same soils and fertility amendments as in the competition study. We selected a total density of 36 plants pot^{-1} for both weed species because this density resulted in equivalent N uptake as corn monoculture at 4 plants pot^{-1} over the period of 35 to 54 d. The ratio of 4 corn plants : 36 weed plants is within the range of corn : weed density ratios that cause yield loss in agricultural fields (Ryan et al. 2010).

Each combination of replacement series (corn : smooth pigweed or corn : giant foxtail replacement series), soil management type (organic or conventional), and harvest date was replicated three times in a single experiment.

Soil Collection. Soil was collected from the Sustainable Agricultural Systems Laboratory's Farming Systems Project (FSP), an experiment comparing organic and conventional management systems established in 1996. The dominant soil series in the FSP are Christiana (fine, kaolinitic, mesic Typic Paleudults), Matapeake (fine-silty, mixed, semiactive, mesic Aquic Hapludults), Keyport (fine, mixed, semiactive, mesic Aquic Hapludults), and Mattapex (fine-silty, mixed, active, mesic Aquic Hapludults) silt loams. Soil was excavated from the plow layer of the conventional chisel-till (CT) system comprising a 3-yr corn–cereal rye (*Secale cereale* L.) cover crop–soybean–winter wheat (*Triticum aestivum* L.)/double-cropped soybean rotation, and the 6-yr organic (ORG) system comprising a corn–cereal rye cover crop–soybean–winter wheat–alfalfa (*Medicago sativa* L.)–alfalfa–alfalfa rotation. In addition to crop rotation differences, the systems differ in fertility management (N, phosphorus [P], and potassium [K] mineral fertilizer in CT vs. alfalfa, poultry litter, and mineral K fertilizer in ORG), weed management (herbicides in CT vs. cultivation in ORG), and tillage type before corn (chisel plowing in CT vs. moldboard plowing in ORG). The different weed management tactics employed in the two systems result in greater weed coverage in the ORG system, which, along with differences in N availability and corn population, contributes to lower yields in the ORG vs. CT system in most years (Cavigelli et al. 2008). A more thorough description of the FSP management history and crop yields can be found in Cavigelli et al. (2008).

Soil from both systems was collected in May 2011, after the cereal rye cover crop was killed using tillage and after P and K fertilizers were applied. A shovel was used to excavate soil from a series of six trenches (1 m long by 0.2 m deep) within each system in each of three blocks. The soil was then coarsely sieved into a large soil wagon containing either the CT or ORG soil. Each soil was homogenized in a large soil mixer, and then sieved through a 6-mm screen. The soils were stored in covered plastic containers at 4 C until they were given a final hand-mixing and placed in pots. Three samples of each soil were air-dried and passed through a 2-mm sieve. Soil inorganic N (NO_3^-–N and NH_4^+–N) was extracted from the air-dried soil samples using 1 M KCl. The filtered extracts were analyzed for NO_3^-–N and NH_4^+–N concentrations using automated colorimetric determination (Mulvaney 1996) (Technicon Autoanalyzer II, Technicon Instruments, Tarrytown, NY). The CT and ORG soil samples were also analyzed for pH and Mehlich 3-extractable nutrient concentrations at A&L Eastern Labs (Richmond, VA). Selected soil properties are summarized in Table 1.

Table 1. Selected fertility properties of soils collected from the surface 20 cm of the conventional chisel-till and organic cropping systems in the Farming Systems Project, Beltsville, MD. Values represent means of three samples collected from each soil prior to fertility amendment. Standard errors are shown in parentheses. Sufficiency ratings are based on University of Maryland Fertility Index Values for agronomic crops (University of Maryland Cooperative Extension 2009).[a]

Soil property	CT	Sufficiency	ORG	Sufficiency
Total N, %	0.14 (0.01)	—	0.17 (0.01)	—
Total C, %	1.38 (0.03)	—	1.73 (0.09)	—
$[NO_3^- + NH_4^+]$–N, g m^{-2}	2.31 (0.16)	—	4.35 (0.30)	—
pH (1 : 1 H_2O)	6.27 (0.03)	A	6.40 (0.06)	A
Mehlich 3 extractable				
P, mg kg^{-1}	79 (3)	H	63 (1)	H
K, mg kg^{-1}	125 (4)	H	140 (5)	H
Mg, mg kg^{-1}	176 (2)	VH	219 (6)	VH
Ca, mg kg^{-1}	1320 (12)	VH	1540 (42)	VH

[a] Abbreviations: CT, chisel-till cropping system; ORG, organic cropping system; A, adequate; H, high; VH, very high.

Species Description. A certified organic 99-d corn hybrid (cultivar 'Blue River 44R57') was used in this experiment. The summer annual weeds smooth pigweed and giant foxtail were selected because they are economically detrimental weeds of the region and important weed species in the FSP (Teasdale et al. 2004). The smooth pigweed and giant foxtail seeds were collected from native populations at BARC and stored at −20 C until planting.

Greenhouse Experiment. The greenhouse corn–weed competition study began in August 2011 when 210 6-L pots, without drain holes (22 cm in height, 21 cm top diam), were filled with 4.54 kg (dry-equivalent mass) each of field-moist CT or ORG soil. We used pots without drain holes to avoid leaching of inorganic N out of the pots. We amended pots with equivalent plant-available N from each N source used in the respective FSP systems: 40.5 mg N kg^{-1} soil as NH_4NO_3 for the CT pots and 40.5 mg N kg^{-1} soil as pelletized poultry litter for the ORG pots. This application rate is equivalent to 120 kg plant-available N ha^{-1}, a rate that is within the range of fertilizer N rates used in U.S. field corn production (USDA-NASS 2010). Pelletized poultry litter was applied at a fresh mass of 2.03 g kg^{-1} soil, which was estimated to provide 40.5 mg plant-available N kg^{-1} soil, assuming 45% of organic N and 90% of NH_4^+–N contained in the product was plant-available during the experiment (Spargo et al. unpublished). Pots were tamped several times after filling to achieve a similar bulk density (final bulk density of ~ 0.9 Mg m^{-3}), leaving approximately 2.5 cm distance between the soil surface and the rim of the pot. For 5 d, pots were watered and weeds emerging from the native soil seedbank were removed.

Corn seeds were evenly spaced on the soil surface and covered with 865 g (dry-equivalent mass) of autoclaved soil (~ 2.5 cm depth) 5 d after the pots were filled. When sowing weed seeds, the potted soil was first topped with 650 g of autoclaved soil; smooth pigweed or giant foxtail seeds were then carefully sprinkled on the surface to provide even spacing, and finally, the remaining 215 g of autoclaved soil (~ 0.63 cm depth) were applied after seeding the smooth pigweed or giant foxtail. The soil used to fill the top 2.5 cm of each pot was autoclaved to sterilize any native weed seeds present. The autoclaved cap extended below the depth at which weed seeds were planted so that planted weeds would emerge sooner than native weeds and facilitate removal of late-emerging weeds from the native seedbank during and after thinning. Total soil dry mass was 5.41 kg pot^{-1}. Both corn and weed seeds were sowed at a higher density than required and thinned to the designated densities. Unplanted control pots containing CT or ORG soil, and the same N rate and autoclaved cap as planted pots, were prepared in triplicate for each of five destructive harvests. Five rather than three harvest dates were included for the unplanted control pots in order to adequately quantify soil N mineralization over the experiment duration.

Pots were arranged on greenhouse benches randomly, and rerandomized two or three times per week, with a 0.3-m minimum spacing between each pot to minimize light competition. Environmental data were collected every 30 min from planting until harvest. Average day and night temperatures in the greenhouse during this experiment were 26.1 C (standard deviation [SD] = 1.0) and 23.7 C (SD = 1.2), respectively. Average daily air humidity and daytime sunlight irradiance were

82.7% (SD = 7.0) and 19.3 W m^{-2} (SD = 10.0), respectively with a 12.5-h day length supplemented by 400 W high-pressure sodium lights for a photoperiod of 16 h. Each pot was watered two or three times per week to field capacity mass, which was calculated based on the water content of each soil at −0.33 bar using a ceramic pressure-plate cell (Klute 1986). An estimated volume of water was added to each pot on the remaining days each week based on the masses of a subsample of pots. The field capacity mass of each pot was adjusted for the fresh mass of plant shoots after every destructive sampling. Two nutrient solutions—1 M KH_2PO_4 and 1 M KCl—were applied at 29 and 36 DAI to provide 40 mg P kg^{-1} soil and 100 mg K kg^{-1} soil, including P and K supplied from the pelletized poultry litter amendment, to all pots. Half of the total volume of each nutrient solution was applied at 29 DAI, and the remaining half at 36 DAI. At 29, 40, and 48 DAI, three replicates of the corn–smooth pigweed and corn–giant foxtail replacement series in each soil were harvested. The final harvest date was selected based on the onset of severe visual N stress symptoms in corn growing in monocultures and mixtures. Corn growth stages at 29, 40, and, 48 DAI were V5, V7, and V8, respectively. Smooth pigweed remained vegetative throughout the experiment and giant foxtail plants began to tiller at 48 DAI. Soil in unplanted control pots was sampled at pot filling, and at 5, 20, 29, 40, and 48 DAI.

At each destructive harvest, plant biomass from each pot was cut at the soil surface and dried at 70 C; masses were then recorded. Five soil cores (2-cm diam, to the full depth of the pot) were taken across the diameter of each planted and control pot and the soil cores from each pot were composited. Soil was passed through a 2-mm sieve, roots were returned to the soil remaining in the pots, and the sieved soil was air-dried. Soil inorganic N was extracted from the air-dried soil using 1 M KCl. The filtered extracts were analyzed for NO_3^-–N and NH_4^+–N concentrations using automated colorimetric determination (Mulvaney 1996) (Technicon Autoanalyzer II, Technicon Instruments). Soil and roots remaining in each pot were stored at 4 C for less than 2 wk until elutriation. Elutriation involved placing the contents of selected pots (three replicates of the monocultures and 0.5 : 0.5 corn : weed mixtures for both soil management types and all harvest dates) into cylindrical cartridges (18 cm in length, 5.5-cm diam, 0.3-mm mesh). The cartridges were then subjected to ~ 60 min of washing with sprayed water in an enclosed, continuously draining, rotating cylinder (Howe's Welding, Ames, IA). The roots were removed from the cartridges and hand-washed to remove soil and gravel. Because washing the roots was a tedious process, we elected to collect roots from only the monocultures and 0.5 : 0.5 corn : weed mixtures. The total roots from each pot (not separated by species) were dried at 70 C and weighed. Dried root and shoot samples were ground separately to pass a 1.0-mm screen using a Christy and Norris 8-inch (20.3-cm) lab mill (Chelmsford, England) or a Foss Cyclotec 1093 sample mill (Haganas, Sweden) and analyzed for tissue N and C concentrations by the combustion method (Horneck and Miller 1998; Pella 1990) (Costech ECS4010, Valencia, CA).

Statistical Analysis. *Soil Inorganic N.* All soil inorganic N concentrations were converted to a mass $area^{-1}$ basis. Soil inorganic N contents of unamended CT and ORG samples were analyzed for statistical difference using an independent two-sample *t* test. Soil inorganic N contents over time in amended, unplanted control pots were modeled using the exponential growth to maximum function:

$$\text{Soil inorganic N} = y_0 + N_{min}(1 - e^{-\lambda T}) \qquad [1]$$

where y_0 is the inorganic N content at the beginning of the study (entered as a fixed value), N_{min} is the mineralizable N pool (estimated by model fitting), λ is the exponential rate constant, and *T* is time in days. A common value for the exponential rate constant was estimated using the pooled CT and ORG data and entered as a fixed value into the individual soil models to reduce potentially confounding effects of variable exponential rate constants on the mineralizable N pool estimates (Mallory and Griffin 2007; Wang et al. 2004). Curve-fitting was performed for this model and all other nonlinear models used in our analysis using the nls function in R (R Development Core Team 2013).

Soil inorganic N content in planted pots was modeled across corn : weed proportions separately for each replacement series and soil management type at 29 DAI using the following exponential decay function:

$$\text{Soil inorganic N} = N_0 e^{-\lambda P_c} \qquad [2]$$

where N_0 is the *y*-intercept, representing the soil inorganic N content in the smooth pigweed or giant foxtail monoculture (entered as a fixed value), λ is the exponential decay constant (estimated by model fitting), and P_c is the proportion of corn. The exponential decay function was not used to analyze soil inorganic N at 40 and 48 DAI because inorganic N contents did not show a trend across corn proportions at these dates.

The effects of replacement series (planted pots only) and soil management type on the soil inorganic N content model parameter estimates were evaluated using 95% confidence intervals calculated on the difference between treatment means (Johnson and Kuby 2008). Two estimates for a given parameter were declared significantly different if the 95% confidence interval of the difference did not overlap with zero.

Monoculture Shoot Biomass and Shoot N Content. Shoot biomass and shoot N content (calculated as the product of total shoot biomass and shoot tissue N concentration for each pot) were converted to mass area^{-1}. ANOVA was performed on total shoot biomass and total shoot N content of the monocultures using SAS Proc Mixed (Version 9.2, SAS Institute, Cary, NC) (SAS Institute 2008). Shoot biomass was square root–transformed to meet the homogeneity of variance assumption. The fixed effects were replacement series, soil management type, harvest date, and their interactions. Random effects were not included in the models. A Tukey test was used for means comparisons.

Replacement Series Indices. Shoot biomass and shoot N content of each species individually, and total shoot biomass and N content of both species combined were modeled across the replacement series using the following functions (de Wit 1960):

$$y_c = (y_{cc} P_c k_c)/[(P_c k_c) + P_w] \quad [3]$$

$$y_w = (y_{ww} P_w k_w)/[(P_w k_w) + P_c] \quad [4]$$

$$y_{total} = y_c + y_w \quad [5]$$

where y_c is the corn shoot biomass or shoot N content in mixture, y_{cc} is the corn shoot biomass or shoot N content in monoculture (entered as a fixed value), k_c is the relative crowding coefficient (RCC) of corn with respect to weed (estimated by model fitting), P_w is the weed proportion, y_w is the weed shoot biomass or shoot N content in mixture, y_{ww} is the weed shoot biomass or shoot N content in monoculture (entered as a fixed value), and k_w is the RCC of weed with respect to corn (estimated by model fitting). RCC values greater than one indicate that the yield (shoot biomass or shoot N content) of a species in mixture was greater than the monoculture yield of that species weighted by the mixture proportion; RCC values less than one indicate that the yield of a species in mixture was less than the proportion-weighted monoculture yield of that species; RCC values equal to one indicate equivalent yield of the species in mixture as the proportion-weighted monoculture yield of that species (Williams and McCarthy 2001). The product of the RCC estimates of two competing species (RCCP) indicates overyielding when significantly greater than one (Hall 1974).

After confirming that RCC estimates were normally distributed, 95% percent confidence intervals were calculated for RCCs and RCCPs. We also used 95% confidence intervals of differences to compare RCC and RCCP estimates between the CT and ORG soils within a particular replacement series–harvest date combination. To calculate the confidence interval of the difference of RCCP estimates, we first computed a variance of the product of two RCC estimates, k_c and k_w, using a first-order Taylor expansion (Goodman 1962). The RCC and RCCP estimates were declared significantly different than one when their 95% confidence intervals did not overlap with one. Significant differences in the RCC and RCCP estimates between CT and ORG soils were reported when the 95% confidence intervals of their difference did not overlap with zero.

Relative yield (RY) and RY total (RYT) were calculated using shoot biomass and shoot N content for each combination of corn : weed proportion, replacement series, soil management type, and harvest date using the following functions (Fowler 1982):

$$RY_c = y_c/(P_c y_{cc}) \quad [6]$$

$$RY_w = y_w/(P_w y_{ww}) \quad [7]$$

$$RYT = P_c RY_c + P_w RY_w \quad [8]$$

where RY_c and RY_w are the RY values of corn and weed, respectively, as measured by shoot biomass or shoot N content, y_c and y_w are the measured corn and weed shoot biomass or shoot N content in mixture, respectively. RY values greater than one indicate that the species' yield in mixture exceeded its proportion-weighted monoculture yield; values less than one indicate that the species' yield in mixture was lower than its proportion-weighted monoculture yield (Williams and McCarthy 2001). RYT values greater than one represent overyielding.

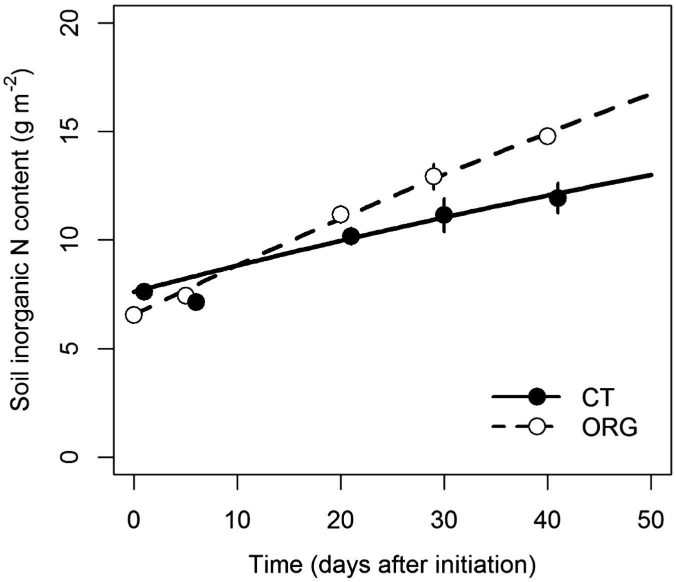

Figure 1. Soil inorganic nitrogen (N) content over time in greenhouse pots containing one of two soil management types with no plants: CT = soil collected from conventional chisel-till system and amended with NH_4NO_3; ORG = soil collected from organic system and amended with pelletized poultry litter. Each point represents the mean inorganic N for a given soil management type and sampling time, vertical lines are ± 1 standard error, and regression curves are exponential models fit to the observations over time (CT: $y = 7.62 + 20.77\ (1 - e^{-0.006T})$; ORG: $y = 6.56 + 39.18\ (1 - e^{-0.006T})$, where T = time in days). Noise was added on the x axis when plotting the means and standard errors to aid in visual interpretation.

Relative yield of mixture (RYM) was calculated using shoot biomass, shoot N content, root biomass, and root N content using the following formula (Wilson 1988):

$$RYM = y_{total}/(P_c y_{cc} + P_w y_{ww}) \qquad [9]$$

where y_{total} is the sum of measured corn and weed shoot biomass, shoot N content, root biomass, or root N content in mixture and the other terms are the same as previously defined. RYM differs from RYT in that it is calculated using the sum of both species' yields, whereas RYT is the sum of both species' RYs. Unlike the RYT, the RYM tends to give greater weight to the species that contributes greater biomass or N content (Williams and McCarthy 2001).

Shoot indices (RY, RYT, shoot RYM) were analyzed by replacement series using ANOVA as described for shoot biomass and shoot N content of monocultures. The fixed effects included corn : weed proportion, soil management type, harvest date, and their interactions. Root RYM results were analyzed in the same way, except that corn : weed proportion was not included as a fixed effect because root data were collected at only one mixture proportion. To determine whether index estimates were significantly different than one, we subtracted one from each index value in our data set and compared the index means to zero using *t* tests constructed in SAS LSMEANS.

Results and Discussion

Soil Inorganic N. The unamended CT soil had lower inorganic N than the unamended ORG soil ($P < 0.05$; Table 1). After NH_4NO_3 and pelletized poultry litter were applied to CT and ORG soils, respectively, soil inorganic N was greater in the CT than in the ORG soil at 0 DAI ($P < 0.05$, Figure 1). Greater soil inorganic N in the CT soil was a result of the NH_4NO_3 amendment being more immediately available than N from the pelletized poultry litter. Over the duration of the experiment, more soil inorganic N became available in the unplanted control pots with ORG soil than in those with CT soil ($P < 0.05$; Figure 1). The greater mineralizable N pool measured in the ORG soil relative to the CT soil in our study is consistent with results of an N mineralization incubation study performed on the same soils without N amendment by Spargo et al. (2011), and with other comparisons of soil mineralizable N in organic and conventional systems (Teasdale et al. 2007; Wander et al. 1994). The proportion of inorganic N as NO_3^-–N in the unplanted control pots ranged from approximately 0.80 to 0.97 and was similar between the two soils at each sampling time (data not shown).

In the planted pots at 29 DAI, soil inorganic N decreased with increasing corn proportion for all combinations of replacement series and soil management types (Figure 2; $P < 0.05$). At this first harvest date, the ORG soil had a greater y-intercept estimate ($P < 0.05$ for corn–smooth pigweed; $P < 0.10$ for corn–giant foxtail), and a smaller decay constant ($P < 0.05$ for both replacement series) than the CT soil, suggesting that more soil inorganic N remained in the ORG soil than in the CT soil across both replacement series. Soil inorganic N in pots containing plants was depleted between 29 and 40 DAI and remained below 0.7 g N m^{-2} across all corn–weed mixtures at 40 and 48 DAI (data for 40 and 48 DAI not shown). The proportion of total inorganic N as NO_3^-–N was unaffected by replacement series, soil management types, or corn : weed proportions, but decreased from approximately 0.88 at 29 DAI to 0.44 at 40 and 48 DAI.

Shoot Biomass and Shoot N Content of Each Species. Corn monocultures produced greater

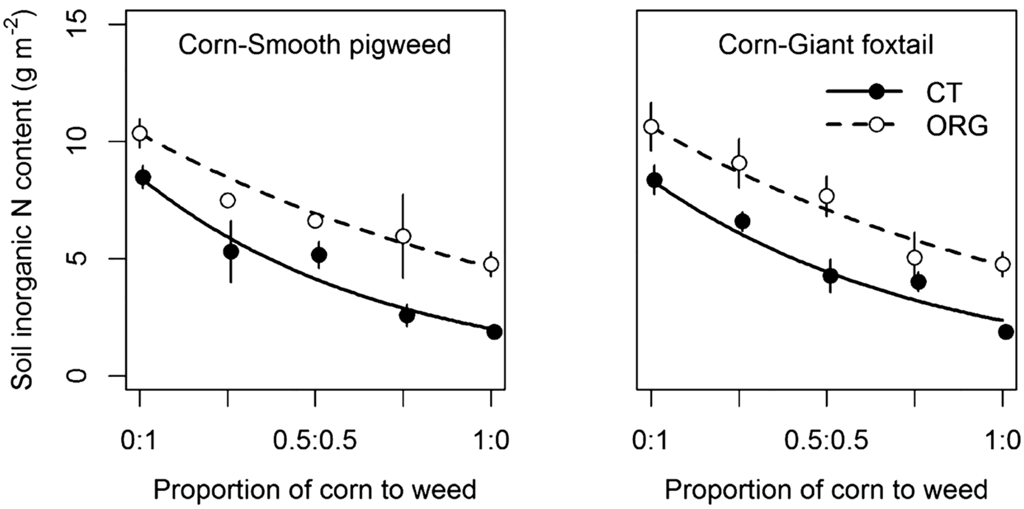

Figure 2. Soil inorganic nitrogen (N) content in greenhouse pots planted with corn–smooth pigweed and corn–giant foxtail replacement series in two soil management types (CT = soil collected from conventional chisel-till system and amended with NH_4NO_3; ORG = soil collected from organic system and amended with pelletized poultry litter) and harvested at 29 d after initiation. Points are mean inorganic N contents, vertical lines are ± 1 standard error, and regression curves are exponential models fit to the observations over the replacement series (corn–smooth pigweed CT: $y = 8.49e^{-1.44P_c}$; corn–smooth pigweed ORG: $= 10.35e^{-0.80P_c}$; corn–giant foxtail CT: $y = 8.36e^{-1.27P_c}$; corn–giant foxtail ORG: $y = 10.64e^{-0.81P_c}$, where P_c is proportion of corn in mixture). Noise was added on the x axis when plotting the means and standard errors to aid in visual interpretation.

biomass than the weed monocultures at 29, 40, and 48 DAI (Figure 3; Table 2; $P < 0.05$), but soil management type did not significantly affect monoculture shoot biomass. Corn shoot biomass increased linearly or with convex curvature as corn proportion increased at all three harvest dates (Figure 3). A linear response (i.e., for both replacement series in the CT soil at 29 DAI) indicates that corn grown in mixture with weeds produced similar biomass as the same number of corn plants grown in monoculture, while a convex response (i.e., for both replacement series in the ORG soil at 29 DAI, and for both replacement series and soil management types at 40 and 48 DAI) indicates that the corn grew better in mixture than expected based on monoculture biomass production. Corn shoot biomass RCC and RY estimates were consistently greater than one, except in the CT soil at 29 DAI (Tables 2 and 3).

The shoot biomass of both weeds decreased linearly or with slight convex curvature with decreasing weed proportion at 29 DAI (Figure 3, left panels). At 40 and 48 DAI, shoot biomass of both weeds decreased linearly or with concave curvature as weed proportion declined (Figure 3, middle and right panels). The concave response indicates that weeds performed worse in mixture with corn than expected based on their monoculture biomass production. The smooth pigweed shoot biomass RCC and RY estimates were similar to one in most cases, except in the ORG soil at 29 DAI when they were greater than one, and in the CT soil at 48 DAI when they were less than one (Tables 2 and 3). The giant foxtail shoot biomass RCC and RY estimates were similar to one (ORG) or greater than one (CT) at the first harvest date. At 40 DAI, the giant foxtail shoot biomass RCC estimates were less than one and the RY estimates were similar to one for both soil management types, whereas at 48 DAI, all giant foxtail shoot biomass RCC and RY estimates were less than one.

Shoot N content of all three monocultures increased from 29 to 40 DAI and remained relatively constant between 40 and 48 DAI (Figure 4; Table 4; $P < 0.05$). Shoot N content of the corn monocultures was significantly greater than shoot N content of the weed monocultures at 29 DAI, but not at 40 and 48 DAI (Figure 4; Table 4; $P < 0.05$). The equivalent shoot N content of monocultures at 40 and 48 DAI indicates that the species densities chosen for this experiment accurately achieved comparable levels of resource acquisition as was planned. Corn, smooth pigweed, and giant foxtail monocultures accumulated greater shoot N in the ORG soil than in the CT soil at 40 and 48 DAI (Figure 4; Table 4; $P < 0.05$), a finding that was consistent with the greater mineralizable N pool that was measured in the ORG vs. CT unplanted control pots (Figure 1). As was the case with shoot biomass, corn shoot N content increased linearly or with convex curvature with increasing corn proportion, while shoot N

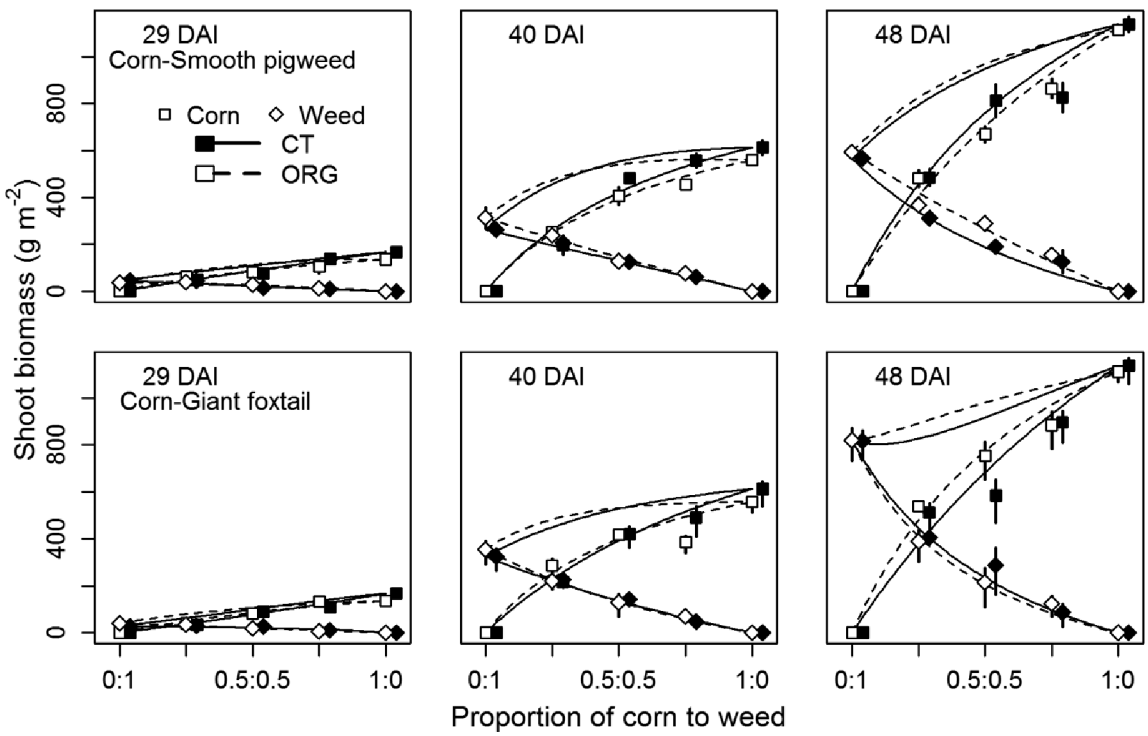

Figure 3. Shoot biomass of corn–smooth pigweed and corn–giant foxtail replacement series grown in two soil management types (CT = soil collected from conventional chisel-till system and amended with NH_4NO_3; ORG = soil collected from organic system and amended with pelletized poultry litter) and harvested at 29, 40, or 48 d after initiation (DAI). The points and error bars represent data means and standard errors, but note that monoculture mean differences were assessed using an ANOVA model. Regression curves are de Wit models fit to the observations. Curves with positive slope represent corn biomass; curves with negative slope represent weed biomass and the upper curves of each plot represent total biomass of both species. Noise was added on the x axis when plotting the means and standard errors to aid in visual interpretation.

content of both weeds decreased linearly or with convex curvature at 29 DAI, and linearly or with concave curvature at 40 and 48 DAI with decreasing weed proportion (Figure 4). The shoot N content RCC and RY estimates also behaved similarly as the shoot biomass RCC and RY estimates in terms of equivalence to unity, except that there were a greater number of weed RCC and RY estimates less than one for shoot N than for shoot biomass at 40 and 48 DAI (Tables 4 and 5).

Relative Competitiveness of Corn, Smooth Pigweed, and Giant Foxtail. Taken together, the shoot biomass and shoot N content replacement series diagrams, RCC estimates, and RY estimates indicate that corn accumulated greater shoot biomass and shoot N in mixture with smooth pigweed or giant foxtail than expected based on its monoculture shoot biomass and shoot N content. The only case in which corn accumulated similar shoot biomass and shoot N in mixture as expected in monoculture was in the CT soil at 29 DAI, and this result may have been due to minimal interaction between the relatively small corn and weeds at the first sampling date (Harper 1977). Although plant densities in this experiment were adjusted so that each species would take up equivalent N in monoculture, corn was more successful at acquiring N at the earliest sampling date (Figure 4, left panels; Table 4) and was more efficient at utilizing N for biomass production at 40 and 48 DAI, as indicated by the greater shoot biomass of corn relative to weeds despite similar shoot N contents. These advantages probably contributed to the greater competitiveness of corn with weeds.

Except for a few cases, smooth pigweed shoot biomass in mixture was similar to the expected shoot biomass based on its monoculture productivity, whereas smooth pigweed shoot N content, giant foxtail shoot biomass, and giant foxtail shoot N content were usually lower in mixture than in expected based on monoculture performance. Smooth pigweed tended to compete better against corn when grown in the ORG soil than in the CT soil, whereas giant foxtail tended to compete better against corn when grown in the CT soil than in the ORG soil, particularly at 29 and 48 DAI. However, at 29 DAI, the weeds were relatively small and soil inorganic N was nonlimiting, so the effects of soil management type on weed shoot biomass and shoot

Table 2. De Wit model parameter estimates and coefficients of determination for shoot biomass of corn–smooth pigweed, and corn–giant foxtail replacement series grown in two soil management types and harvested on three dates: 29, 40, or 48 d after initiation. Values in parentheses are standard errors.[a]

		Corn				Weed					
Series	Soil	Monoculture biomass, g m^{-2}	RCC	EU[b]	R^2	Monoculture biomass, g m^{-2}	RCC[c]	EU	R^2	RCCP[d]	EU
29 DAI											
Corn–SP	CT	168 (8)	1.09 (0.19)	= 1	0.82	46 (2)	0.98 (0.23)	= 1	0.89	1.06	= 1
	ORG	137 (8)	1.79 (0.47)	> 1	0.83	37 (7)	2.44 (0.75)	> 1	0.87	4.37	= 1
Corn–GF	CT	168 (8)	0.87 (0.14)	= 1	0.85	28 (2)	3.54 (1.17) a	> 1	0.87	3.07	= 1
	ORG	137 (8)	1.68 (0.40)	> 1	0.88	41 (5)	1.00 (0.36) b	= 1	0.76	1.67	= 1
40 DAI											
Corn–SP	CT	613 (30)	2.22 (0.38)	> 1	0.93	264 (4)	0.98 (0.11)	= 1	0.97	2.16	> 1
	ORG	559 (19)	2.41 (0.28)	> 1	0.97	313 (43)	0.87 (0.15)	= 1	0.93	2.10	> 1
Corn–GF	CT	613 (30)	1.79 (0.26)	> 1	0.94	324 (34)	0.72 (0.08)	< 1	0.97	1.29	= 1
	ORG	559 (19)	2.53 (0.46)	> 1	0.92	354 (36)	0.59 (0.09)	< 1	0.94	1.50	= 1
48 DAI											
Corn–SP	CT	1,138 (31)	2.01 (0.29)	> 1	0.95	567 (9)	0.50 (0.06) b	< 1	0.97	1.00	= 1
	ORG	1,113 (18)	1.72 (0.16)	> 1	0.98	594 (10)	0.81 (0.08) a	= 1	0.97	1.39	> 1
Corn–GF	CT	1,138 (31)	1.50 (0.21) b	> 1	0.95	818 (42)	0.41 (0.05)	< 1	0.96	0.60	< 1
	ORG	1,113 (18)	2.29 (0.25) a	> 1	0.97	821 (50)	0.33 (0.04)	< 1	0.96	0.76	= 1

[a] Abbreviations: RCC, relative crowding coefficient; EU, equivalence to unity; RCCP, relative crowding coefficient product; DAI, days after initiation; SP, smooth pigweed; GF, giant foxtail; CT, soil collected from conventional chisel-till system and amended with NH_4NO_3; ORG, soil collected from organic system and amended with pelletized poultry litter.

[b] RCCs and RCCPs that are significantly less than one, equal to one, or greater than one ($P < 0.05$) are indicated with < 1, = 1, or > 1, respectively.

[c] Different lowercase letters indicate significant differences ($P < 0.05$) in RCC estimates between the two soil management types for the same species, replacement series and harvest date.

[d] No significant differences were detected in estimates of RCCP between the two soil management types within each replacement series and harvest date.

Table 3. Shoot biomass relative yield of corn, relative yield of weed, relative yield total and relative yield of mixture values for corn–smooth pigweed and corn–giant foxtail replacement series grown in two soil management types and harvested on three dates: 29, 40, or 48 d after initiation. Means shown are averaged across corn : weed proportions.[a]

Series	Soil	RY_c	EU[b]	RY_w[c]	EU	RYT	EU	RYM	EU
29 DAI									
Corn–SP	CT	1.07 (0.10)	= 1	0.96 (0.12) b	= 1	1.04 (0.09) b	= 1	1.06 (0.08) b	= 1
	ORG	1.35 (0.16)	> 1	1.42 (0.10) a	> 1	1.33 (0.10) a	> 1	1.32 (0.12) a	> 1
Corn–GF	CT	0.91 (0.10)	= 1	1.60 (0.18) a	> 1	1.26 (0.08)	> 1	1.03 (0.07)	= 1
	ORG	1.20 (0.13)	> 1	0.91 (0.18) b	= 1	1.11 (0.13)	= 1	1.19 (0.12)	> 1
40 DAI									
Corn–SP	CT	1.36 (0.09)	> 1	0.97 (0.07)	= 1	1.17 (0.04)	> 1	1.24 (0.05)	> 1
	ORG	1.45 (0.12)	> 1	0.95 (0.05)	= 1	1.14 (0.03)	> 1	1.21 (0.04)	> 1
Corn–GF	CT	1.28 (0.07)	> 1	0.80 (0.06)	= 1	1.04 (0.04)	= 1	1.10 (0.04)	= 1
	ORG	1.49 (0.17)	> 1	0.79 (0.08)	= 1	1.05 (0.06)	= 1	1.12 (0.06)	= 1
48 DAI									
Corn–SP	CT	1.37 (0.12)	> 1	0.77 (0.11)	< 1	0.99 (0.02)	= 1	1.09 (0.04)	= 1
	ORG	1.32 (0.11)	> 1	0.95 (0.06)	= 1	1.06 (0.02)	= 1	1.11 (0.03)	= 1
Corn–GF	CT	1.29 (0.14)	> 1	0.60 (0.08)	< 1	0.90 (0.02)	= 1	0.95 (0.03)	= 1
	ORG	1.45 (0.13)	> 1	0.59 (0.07)	< 1	0.95 (0.02)	= 1	1.00 (0.02)	= 1

[a] Abbreviations: RY_c, relative yield of corn; EU, equivalence to unity; RY_w, relative yield of weed; RYT, relative yield total; RYM, relative yield of mixture; DAI, days after initiation; SP, smooth pigweed; GF, giant foxtail; CT, soil collected from conventional chisel-till system and amended with NH_4NO_3; ORG, soil collected from organic system and amended with pelletized poultry litter.

[b] Relative yield, RYT, and RYM values that are significantly less than one, equal to one, or greater than one ($P < 0.05$) are indicated as such with < 1, = 1, or > 1, respectively.

[c] Different lowercase letters indicate significant differences ($P < 0.05$) in index values between the two soil management types within the same replacement series, harvest date and index.

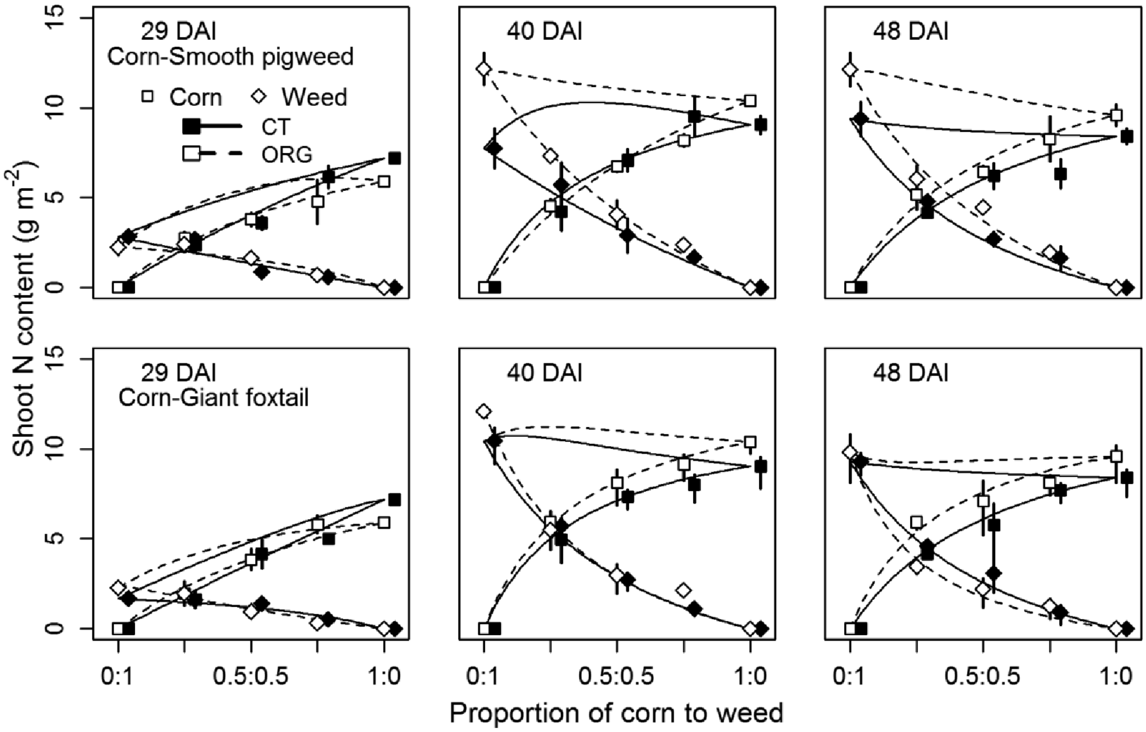

Figure 4. Shoot nitrogen (N) content of corn–smooth pigweed and corn–giant foxtail replacement series grown in two soil management types (CT = soil collected from conventional chisel-till system and amended with NH_4NO_3; ORG = soil collected from organic system and amended with pelletized poultry litter) and harvested at 29, 40, or 48 d after initiation (DAI). The points and error bars represent data means and standard errors, but note that monoculture mean differences were assessed using an ANOVA model. Regression curves are de Wit models fit to the observations. Curves with positive slope represent corn shoot N content; curves with negative slope represent weed shoot N content and the upper curves of each plot represent total shoot N content of both species. Noise was added on the x axis when plotting the means and standard errors to aid in visual interpretation.

N content across the replacement series do not necessarily reflect differences in competitive ability and may not be biologically meaningful. That said, other research has shown that high levels of soil inorganic N enhance the competitiveness of redroot pigweed, a close relative of smooth pigweed (Blackshaw and Brandt 2008), whereas green foxtail [*Setaria viridis* (L.) Beauv.] a relative of giant foxtail, tends to be less responsive to added inorganic N than redroot pigweed (Blackshaw et al. 2003). Therefore, effects of soil management type on relative competitiveness of smooth pigweed and giant foxtail could be caused by greater N availability in the ORG soil than in the CT soil. Overall, there were fewer cases of RCC and RY estimates significantly less than one for smooth pigweed than for giant foxtail, suggesting that smooth pigweed is a stronger competitor against corn than giant foxtail. This finding corresponds with weed management literature that reports smooth pigweed to be a more competitive weed in corn than giant foxtail on an equivalent density basis (Curran et al. 2013; Marose et al. 1991).

Shoot and Root Biomass and N Content of Mixtures. The responses of total shoot biomass across corn : weed proportions typically displayed convex curvature, although there were a few cases where the total shoot biomass increased linearly (i.e., for both replacement series in the CT soil at 29 DAI, and for corn–giant foxtail in the ORG soil at 48 DAI) or with concave curvature (i.e., for corn–giant foxtail in the CT soil at 48 DAI), with increasing corn proportion (Figure 3). The corn–smooth pigweed shoot biomass RCCP, RYT, and RYM estimates were greater than one for both soil management types at 40 DAI and selected indices demonstrated overyielding for the ORG soil at the other harvest dates (Tables 2 and 3). The corn–giant foxtail shoot biomass RCCP, RYT, and RYM estimates tended to be equal to one for most soil management type–harvest date combinations.

The replacement series diagrams demonstrated convex curvature of total shoot N content for both replacement series in the ORG soil at 29 DAI, and for the corn–smooth pigweed replacement series in the CT soil at 40 DAI (Figure 4). Except in these cases, the total shoot N content formed a straight line across the replacement series. The shoot N content RCCP, RYT, and RYM estimates tended to be greater than one at 29 DAI, but equivalent to one at

Table 4. De Wit model parameter estimates and coefficients of determination for shoot nitrogen content of corn–smooth pigweed, and corn–giant foxtail replacement series grown in two soil management types and harvested on three dates: 29, 40, or 48 d after initiation. Values in parentheses are standard errors.[a]

		Corn				Weed					
Series	Soil	Monoculture N content, g m^{-2}	RCC	EU[b]	R^2	Monoculture N content, g m^{-2}	RCC[c]	EU	R^2	RCCP[d]	EU
		29 DAI									
Corn–SP	CT	7.2 (0.3)	1.28 (0.19)	= 1	0.84	2.8 (0.1)	0.90 (0.20)	= 1	0.90	1.15	= 1
	ORG	5.9 (0.3)	2.08 (0.50)	> 1	0.86	2.3 (0.5)	2.27 (0.71)	> 1	0.86	4.72	> 1
Corn–GF	CT	7.2 (0.3)	1.04 (0.17)	= 1	0.93	1.7 (0.1)	2.47 (0.65) a	> 1	0.89	2.56	> 1
	ORG	5.9 (0.3)	1.92 (0.39)	> 1	0.91	2.3 (0.2)	0.88 (0.29) b	= 1	0.79	1.69	= 1
		40 DAI									
Corn–SP	CT	9.0 (0.5)	3.31 (0.87)	> 1	0.88	7.7 (1.1)	0.75 (0.18)	= 1	0.87	2.47	= 1
	ORG	10.4 (0.3)	1.93 (0.19)	> 1	0.98	12.2 (0.9)	0.53 (0.06)	< 1	0.97	1.03	= 1
Corn–GF	CT	9.0 (0.5)	3.73 (0.70)	> 1	0.93	10.4 (0.7)	0.38 (0.04)	< 1	0.98	1.42	= 1
	ORG	10.4 (0.3)	3.72 (0.50)	> 1	0.96	12.1 (0.2)	0.32 (0.03)	< 1	0.98	1.18	= 1
		48 DAI									
Corn–SP	CT	8.4 (0.4)	2.53 (0.51)	> 1	0.90	9.4 (0.9)	0.39 (0.06)	< 1	0.95	0.99	= 1
	ORG	9.6 (0.6)	2.76 (0.63)	> 1	0.88	12.1 (0.9)	0.44 (0.05)	< 1	0.96	1.21	= 1
Corn–GF	CT	8.4 (0.4)	2.66 (0.52) b	> 1	0.91	9.3 (0.4)	0.38 (0.04)	< 1	0.97	1.01	= 1
	ORG	9.6 (0.6)	3.85 (0.86) a	> 1	0.90	9.8 (1.0)	0.22 (0.04)	< 1	0.95	0.84	= 1

[a] Abbreviations: N, nitrogen; RCC, relative crowding coefficient; EU, equivalence to unity; RCCP, relative crowding coefficient product; DAI, days after initiation; SP, smooth pigweed; GF, giant foxtail; CT, soil collected from conventional chisel-till system and amended with NH_4NO_3; ORG, soil collected from organic system and amended with pelletized poultry litter.

[b] RCCs and RCCPs that are significantly less than one, equal to one, or greater than one ($P < 0.05$) are indicated with < 1, = 1, or > 1, respectively.

[c] Different lowercase letters indicate significant differences ($P < 0.05$) in RCC estimates between the two soil management types for the same species, replacement series and harvest date.

[d] No significant differences were detected in estimates of RCCP between the two soil management types within each replacement series and harvest date.

40 and 48 DAI for most replacement series–soil management type combinations (Tables 4 and 5). Overall, there were few effects of soil management type on shoot N RCCP, RYT, or RYM, but total N uptake tended to be greater overall in the ORG soil than in the CT soil at 40 and 48 DAI. These observations suggest that the greater crop tolerance to weeds observed in organic vs. conventional systems may be due to a larger plant-available N pool in the organic systems rather than due to differences in N resource partitioning (Ryan et al. 2010).

ANOVA showed that soil management type did not affect the RYM values for root parameters for any replacement series–harvest date combinations. In general, RYM for root biomass and root N content increased from values mostly less than one at 29 DAI to values mostly equal to one at 40 and 48 DAI (Table 6). Only the corn–smooth pigweed mixtures showed overyielding of root biomass (RYM > 1) at 40 DAI.

Evidence of Resource Partitioning. We measured overyielding in corn–weed mixtures grown in soils with contrasting management to evaluate whether N resource partitioning may contribute to greater weed tolerance in organic systems relative to conventional systems. The replacement series indices provided some evidence for overyielding at 29 DAI for corn–smooth pigweed mixtures in the ORG soil, and for corn–giant foxtail mixtures in the CT and ORG soils. At 40 DAI, the replacement series indices provided evidence of corn–smooth pigweed shoot biomass overyielding in both soils and shoot N overyielding in the CT soil.

Overyielding can be used to indicate resource partitioning among two species if the species are actively competing over the resource of interest (i.e., demand for resource equals supply) (Sackville Hamilton 1994; Taylor and Aarssen 1989). At 29 DAI, inorganic N supply probably exceeded demand as at least 1.5 g inorganic N m^{-2} remained in all mixtures and plants continued to accumulate N after this harvest date. Therefore, although the replacement series indices suggested overyielding, the lack of inorganic N limitation implies that overyielding cannot be interpreted as evidence of

Table 5. Shoot nitrogen content relative yield of corn, relative yield of weed, relative yield total and relative yield of mixture values for corn–smooth pigweed and corn–giant foxtail replacement series grown in two soil management types and harvested on three dates: 29, 40, or 48 d after initiation. Means shown are averaged across corn : weed proportions.[a]

Series	Soil	RY_c	EU[b]	RY_w[c]	EU	RYT	EU	RYM	EU
		29 DAI							
Corn–SP	CT	1.15 (0.09)	= 1	0.91 (0.11) b	= 1	1.05 (0.08) b	= 1	1.09 (0.07) b	= 1
	ORG	1.41 (0.16)	> 1	1.37 (0.10) a	> 1	1.34 (0.10) a	> 1	1.35 (0.12) a	> 1
Corn–GF	CT	1.00 (0.11)	= 1	1.40 (0.16) a	> 1	1.20 (0.07)	> 1	1.09 (0.07)	= 1
	ORG	1.31 (0.13)	> 1	0.86 (0.16) b	= 1	1.13 (0.12)	> 1	1.21 (0.11)	> 1
		40 DAI							
Corn–SP	CT	1.61 (0.16)	> 1	0.87 (0.11)	= 1	1.21 (0.07)	> 1	1.23 (0.07) a	> 1
	ORG	1.36 (0.11)	> 1	0.75 (0.05)	< 1	1.00 (0.03)	= 1	0.98 (0.03) b	= 1
Corn–GF	CT	1.67 (0.18)	> 1	0.56 (0.05)	< 1	1.05 (0.03)	= 1	1.02 (0.03)	= 1
	ORG	1.67 (0.18)	> 1	0.60 (0.05)	< 1	1.04 (0.02)	= 1	1.00 (0.02)	= 1
		48 DAI							
Corn–SP	CT	1.49 (0.16)	> 1	0.65 (0.08)	< 1	0.99 (0.04)	= 1	0.97 (0.03)	= 1
	ORG	1.55 (0.19)	> 1	0.68 (0.04)	< 1	1.03 (0.04)	= 1	0.99 (0.03)	= 1
Corn–GF	CT	1.52 (0.14)	> 1	0.57 (0.08)	< 1	1.01 (0.03)	= 1	0.99 (0.02)	= 1
	ORG	1.69 (0.21)	> 1	0.48 (0.06)	< 1	0.97 (0.03)	= 1	0.96 (0.03)	= 1

[a] Abbreviations: RY_c, relative yield of corn; EU, equivalence to unity; RY_w, relative yield of weed; RYT, relative yield total; RYM, relative yield of mixture; DAI, days after initiation; SP, smooth pigweed; GF, giant foxtail; CT, soil collected from conventional chisel-till system and amended with NH_4NO_3; ORG, soil collected from organic system and amended with pelletized poultry litter.

[b] Relative yield, RYT, and RYM values that are significantly less than one, equal to one, or greater than one ($P < 0.05$) are indicated as such with < 1, = 1, or > 1, respectively.

[c] Different lowercase letters indicate significant differences ($P < 0.05$) in index values between the two soil management types within the same replacement series, harvest date and index.

resource partitioning within the replacement series design. The overyielding at 29 DAI may be attributed instead to the greater quantity of uncontested soil inorganic N in the mixtures relative to corn monocultures (Figure 2). At 40 DAI, soil inorganic N had become depleted in the pots, and plant shoot N uptake ceased between 40 and 48 DAI. The high degree of resource depletion at 48 DAI probably restricted opportunities for mixtures to more efficiently acquire N than monocultures, resulting in very little evidence for overyielding at this harvest date. Because the harvest at 40 DAI took place after the onset of inorganic N depletion, but before inorganic N supply completely limited plant N accumulation, this harvest date most accurately reflects conditions in which plant N demands equaled inorganic N supply. Therefore, the shoot biomass and shoot N overyielding observed in corn–smooth pigweed mixtures at 40 DAI provides evidence of N resource partitioning. However, the replacement series indices (RCCP, RYT, RYM) provided no evidence that resource partitioning occurred to a greater extent in the ORG soil than in the CT soil at this harvest date.

Table 6. Root biomass and root nitrogen content relative yield of mixture values for corn–smooth pigweed and corn–giant foxtail replacement series harvested on three dates: 29, 40, or 48 d after initiation. Root parameters were measured on 0.5 : 0.5 corn : weed mixtures and monocultures. Relative yield of mixture values were averaged across soil management types.[a]

	Root biomass		Root N content	
Series	RYM	EU[b]	RYM	EU
	29 DAI			
Corn–SP	0.58 (0.11)	< 1	0.53 (0.14)	< 1
Corn–GF	0.81 (0.09)	< 1	1.07 (0.19)	= 1
	40 DAI			
Corn–SP	1.43 (0.15)	> 1	1.30 (0.17)	= 1
Corn–GF	1.14 (0.05)	= 1	0.91 (0.11)	= 1
	48 DAI			
Corn–SP	1.16 (0.06)	= 1	1.26 (0.18)	= 1
Corn–GF	0.97 (0.06)	= 1	0.85 (0.14)	= 1

[a] Abbreviations: N, nitrogen; RYM, relative yield of mixture; EU, equivalence to unity; DAI, days after initiation; SP, smooth pigweed; GF, giant foxtail.

[b] RYM values that are significantly less than one, equal to one, or greater than one ($P < 0.05$) are indicated as such with < 1, = 1, or > 1, respectively.

Although we did not test specific mechanisms of resource partitioning in this study, the fact that the corn–smooth pigweed root biomass RYM also exceeded one at 40 DAI suggests that corn and smooth pigweed roots may have explored different soil regions within each pot. Small-seeded species such as redroot pigweed have been shown to compete effectively with larger-seeded species by producing longer, narrower roots that increase in length more quickly than roots of larger-seeded species (Siebert and Pearce 1993). It is possible that smaller smooth pigweed roots in our study were able to access soil areas inaccessible to larger corn roots. This complementary spatial distribution of corn and smooth pigweed roots may have allowed the two species to acquire inorganic N from different locations. The occurrence of resource partitioning in corn–smooth pigweed mixtures but not in corn–giant foxtail mixtures suggests that shifts in weed community composition due to agricultural management (Davis et al. 2005; Menalled et al. 2001) may influence the degree of N resource partitioning.

In summary, replacement series indices provided some evidence for N resource partitioning by corn–smooth pigweed mixtures at the onset of soil inorganic N limitation, which may reflect the ability of corn and smooth pigweed to acquire inorganic N from different soil regions. We did not observe clear differences in the extent of N resource partitioning between the soil management types during the initial stages of corn growth. Soil conditions in the field are more complex than those in this pot experiment because of greater soil heterogeneity, a larger reservoir of soil resources that would not be readily depleted, and a prolonged period of competition for the full cropping season. Therefore, greater N resource partitioning between competing species may be observed in field experiments, though not in pot experiments (Ellern et al. 1970). Our finding that the ORG soil provided greater plant-available N than the CT soil supports the hypothesis that soils under organic management could produce greater crop growth than conventionally managed soils despite higher weed biomass because of a larger soil mineralizable N pool (Ryan et al. 2010). Future research should investigate spatial/temporal factors and weed community composition differences in the field that could affect the extent of resource partitioning in cropping systems, as well as the role of the mineralizable N pool size in determining crop response to weed pressure.

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