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**COVER CROP MANAGEMENT EFFECTS ON
WEED COMMUNITIES IN A PLANTING GREEN
SYSTEM**

A Thesis in

Agronomy

by

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Abstract

Integrated weed management (IWM) is essential for managing herbicide resistant weeds in no-till cropping systems. The use of cover crops as an integrated weed management tactic provides an opportunity to reduce herbicide selection pressure and increase control of herbicide resistant species. Cover crop management decisions made by growers depend on agronomic tradeoffs and input costs associated with cover cropping tactics. Planting green is a cover crop management tactic where cover crop termination is delayed until cash crop planting. In Pennsylvania, there has been increased interest in planting green. We investigated the effects of cereal rye seeding rates on weed suppression when using planting green tactics at two locations in Pennsylvania and one location in Delaware. Weed population responses were evaluated across four cereal rye seeding rate treatments: 0, 51, 101, 135 kg ha⁻¹. Our results found that the presence of cereal rye improved weed suppression compared to the control treatment. Weed suppression was similar across cereal rye seeding rates 51 – 135 kg ha⁻¹.

An additional field experiment evaluated the effects of cover crop termination timing and reduced herbicide inputs on weed suppression. This study was conducted at Rock Springs, PA across three growing seasons and included two cover crop termination treatments: planting green with reduced herbicide use and standard cover crop termination with standard herbicide use. Our results found that planting green provided similar summer annual weed suppression compared to standard cover crop termination. However, standard cover crop termination improved horseweed control compared to the planting green treatment.

A third experiment investigated the effects cover crop surface mulch could have on weed community composition in a greenhouse experiment. Seedling establishment and resource allocation of ten weed and two crop species was evaluated across a seed mass gradient and cereal rye surface mulch levels, including 0, 3,360, 6,720, and 10,080 kg ha⁻¹. Our results demonstrated that seed mass was positively correlated with seedling establishment rates under increasing cereal rye mulch levels. In response to increasing cereal rye surface mulch, resource allocation in broad-leaved species were diverted to aboveground biomass, particularly hypocotyl elongation, but surface mulch levels had no significant effect on monocotyledon species.

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Chapter 1

Introduction

Reliance on herbicide-based weed control in no-till field crop production has increased selection pressure for evolution of herbicide resistance (Mortensen et al., 2012; Norsworthy et al., 2012). Herbicides are a cost-effective weed management tool (Mortensen et al., 2012; Norsworthy et al., 2012). However, an integrated weed management (IWM) approach, in which multiple complementary weed management tactics are implemented, is necessary to control herbicide resistant weed species that are now a widespread problem (Liebman, 2018; Mortensen et al., 2012; Norsworthy et al., 2012). Diversifying weed management tactics reduces selection pressure for evolution of resistance to herbicides (Mortensen et al., 2012; Norsworthy et al., 2012), by altering the intensity, timing, and duration of disturbance, which influences weed community composition and abundance (Booth & Swanton, 2002; Smith & Mortensen, 2017).

Cover crops are integrated into no-till field crop production systems to provide several agronomic benefits and have been proven useful for weed management. Several studies have attributed reduced herbicide selection pressure to weed suppression from cover crop residues, where the size of weed populations (Loux et al., 2017; Montgomery et al., 2018; Wiggins et al., 2015) and the size of individual within populations are lower at time of herbicide exposure (Bunchek et al., 2020; Wallace et al., 2019). Additionally, Teasdale et al. (2005) found that weed seedling control could be obtained at lower herbicide concentrations when cover crop residues and herbicides were integrated.

Cover crop management tactics used by growers depend on consideration of ecosystem services, input costs, and cash crop yield impacts. Intensifying cover crop management tactics to maximize cover crop biomass has been shown to improve weed suppression potential and promote longer windows for effective post-emergent herbicide applications (Bunchek et al., 2020; Wallace et al., 2019). In the Mid-Atlantic region, interest in using planting green tactics has increased in no-till systems. Planting green is a tactic in which cover crop termination is delayed until cash crop planting, which enables more cover crop biomass production, thereby prolonging interspecific resource competition with weeds that have overlapping life cycles (Reed et al., 2019). Previous studies have found that increasing growing degree days via earlier seeding date and delayed termination timing (Essman et al., 2020; Feyereisen et al., 2006; Reed et al.,

2019; Schramski et al., 2021; Vollmer et al., 2020) and high fall plant-available nitrogen increase the biomass potential of cereal rye (*Secale cereale* L.), which is the most commonly used cover crop species in grain systems (Mirsky et al., 2017). Some studies have reported that seeding rates have limited impact on total biomass production of cereal rye (Bish et al., 2021; Haramoto, 2019; Ryan et al., 2011). However, studies have also observed a correlation between weed suppression and cereal rye ground cover, which can be influenced by seeding rate and delayed termination (Haramoto, 2019; Schramski et al., 2021). These studies suggest that intensifying cover crop management with planting green tactics has the potential to reduce herbicide and other weed management input costs while maintaining weed control.

Cover crop surface residues suppress annual weeds at vulnerable life-history stages, including from germination to seedling establishment (Leishman et al., 2000; Fenner & Thompson, 2005). Germinated weed seeds must endure low light conditions, phytotoxin exudates, and altered soil moisture and temperature, penetrating the physical barrier created by cover crop residue (Mirsky et al., 2013). Direct and indirect effects of cover crop residue on seedling establishment rates are amplified in systems that maximize biomass production, creating a stronger selection pressure and influencing weed community assembly (Mirsky et al., 2013). Relative fitness of weed species within cover crop residues is likely a function of seed mass because of relationships between seed mass and seedling survival under environmental stress. Previous studies have found that large-seeded species increase survival under carbon deficits created by low light conditions, which was attributed to larger seed reserves and initial seedling size (Ganade & Westoby, 1999; Kidson & Westoby, 2000; Leishman & Westoby, 1994; Westoby et al., 1996). Small-seeded species are known to have a relative fitness advantage when resources are not limited due to higher relative growth rates after establishment (Ganade & Westoby, 1999).

Resource limitation in cover crop residues should induce functional equilibrium of biomass allocation in establishing weed seedlings, in which relatively more biomass is allocated to structures that increase acquisition of the limiting factor (Poorter et al., 2012). Biomass allocation to hypocotyl elongation, a well-known response to low light conditions for dicotyledons, can increase chances of survival to plant establishment (Ballaré et al., 1991; Bruce et al., 2006; Ganade & Westoby, 1999). However, due to limited seed reserves during the

seedling establishment phase, cover crop residues may decrease seedling establishment in small-seeded species. Weed seedling survival in cover crop residues may still result in reduced fitness due to resource depletion, which can increase susceptibility of seedlings to additional management tactics (Ganade & Westoby, 1999).

Growers need information about the agronomic tradeoffs associated with planting green tactics that influence weed management and agronomic goals. Given that planting green tactics will have varying impacts on weed suppression at a species level, a better understanding of ecological mechanisms that determine seedling survival and weed community assembly is necessary for effective long-term weed control. My research addresses these questions to improve our knowledge of weed management while using planting green tactics. In my first chapter, I report on studies that explore the effects of cereal rye seeding rates and reduced herbicide inputs on weed suppression and cash crop yields in no-till soybean systems that employ planting green tactics. In my second chapter, I report on a study that investigates the effects of cereal rye surface residue and weed seed mass on seedling establishment and resource allocation patterns.

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Chapter 2

Fine-tuning Integrated Weed Management Tactics in Cover Crop Based, No-Till Soybean Production

Cover crop-based integrated weed management (IWM) provides an opportunity in no-till cropping systems to reduce herbicide selection pressure and improve weed control efficacy. Cover crop management intensification may facilitate reduced herbicide inputs while maintaining crop protection. In the Mid-Atlantic region, there has been increased interest in planting green, a tactic in which cover crop management is intensified by delaying cover crop termination until cash crop planting. We investigated the effects of cereal rye seeding rates and reduced herbicide inputs on weed control and crop performance when planting green in two field experiments. The cereal rye seeding rate experiment was replicated at five site-years across 2019 and 2020 growing seasons using three locations: Rock Springs, PA, Landisville, PA, and Georgetown, DE. In this study, population-level weed responses were evaluated across four cereal rye seeding rates: 0, 51, 101, 135 kg ha⁻¹. The reduced-herbicide input experiment was conducted at Rock Springs, PA within a long-term dairy cropping systems study for three growing seasons (2019 – 2021) to evaluate population-level weed responses to delayed cover crop termination (i.e., planting green) and reduced herbicide inputs compared to standard cover crop termination timing and use of preemergence herbicide programs. The seeding rate experiment showed that integrating cereal rye in the fall significantly improved weed control compared to the control, but no differences in weed suppression potential were found across cereal rye seeding rate treatments (51 – 135 kg ha⁻¹). Results of the reduced-herbicide input experiment results showed that planting green and reduced herbicide inputs provided similar summer annual weed control but reduced horseweed (*Erigeron canadensis*) control compared to standard cover crop termination and preemergence herbicide programs. Our results suggest planting green offers opportunities to reduce herbicide inputs and cereal rye seeding rates. However, when planting green, weed control is likely weed species specific and requires an adaptive IPM approach that includes effective herbicide sites-of-action to herbicide resistant species.

Introduction

Glyphosate and multiple herbicide-resistant weeds are a widespread problem in agronomic no-till cropping systems (Mortensen et al., 2012; Norsworthy et al., 2012). Currently, stacked-trait transgenic seed technologies that facilitate use of additional herbicide modes-of-action are being deployed to maintain weed control performance. Integrated weed management (IWM) strategies that utilize multiple complementary weed control tactics are essential for reducing herbicide selection pressure for evolution of herbicide resistance (Liebman, 2018; Norsworthy et al., 2012). Effective combinations of herbicide-based and cultural weed control tactics are needed in conservation tillage systems.

Cover crops are increasingly integrated in annual cropping systems to improve soil health (Schipanski et al., 2014), but cover crop management tactics used by growers that target ecosystem services may have agronomic tradeoffs. Currently, there is increasing interest in intensifying cover crop management within the Mid-Atlantic region by using planting green tactics in no-till systems. Planting green is the delay of cover crop termination until cash crop planting, which enables more growth and biomass production than typical pre-plant burndown termination practices (Reed et al., 2019). However, excessive cover crop surface residues can also reduce stand establishment and early-season growth of cash crops. Some growers use lower CC seeding rates to prevent residue management challenges at planting (Reed et al., 2019; Haramoto, 2019).

Among cover crop species, cereal rye (*Secale cereale* L.) is the most common in the Mid-Atlantic region because of its winter hardiness, nitrogen scavenging potential, and high biomass production compared to other cover crop species (Mirsky et al., 2009; Reed et al., 2019). Increasing cover crop biomass can improve weed suppression potential and facilitate longer windows for effective post-emergent herbicide applications (Wallace et al., 2019; Bunck et al., 2020). Previous studies have found that increasing growing degree days via an earlier seeding and delayed termination date (Essman et al., 2020; Feyereisen et al., 2006; Reed et al., 2019; Schramski et al., 2021; Vollmer et al., 2020) and higher plant-available nitrogen in fall increase cereal rye biomass potential (Mirsky et al., 2017). Previous studies have also found that cereal rye seeding rate has limited impact on total biomass (Bish et al., 2021; Ryan et al., 2011, Haramoto, 2019), which suggests that lower seeding rates in planting green scenarios may

provide weed suppression services while maintaining lower cover crop seeding costs. However, late fall and early spring ground cover is also positively correlated to winter- (Wallace et al., 2019) and summer- annual weed suppression (Ryan et al., 2011), and increasing cereal rye seeding rates have been shown to increase ground cover (Haramoto, 2019; Schramski et al., 2021).

Cover crops can be an effective cultural weed control tactic in no-till field crop production (Beam et al., 2021; Desimini et al., 2020; Pittman et al., 2019; Schramski et al., 2021), particularly when employed in combination with herbicide-based tactics (Essman et al., 2020; Vollmer et al., 2020). It has been suggested that intensification of cover crop management tactics, such as planting green, may facilitate reduced herbicide inputs while maintaining crop protection goals (Bunchek et al., 2020). However, the efficacy of this strategy is dependent on species traits within the community, such as herbicide-resistance level, emergence patterns, and establishment rates in surface mulch (Bunchek et al., 2020; Essman et al., 2020; Ficks et al., 2021).

Increased understanding of cereal rye seeding rate effects on weed suppression and the role of delayed termination in facilitating reductions in herbicide inputs are needed to identify tradeoffs between weed management input costs and weed control outcomes (Bunchek et al., 2020). We conducted two complementary field experiments in the context of planting green management practices. In our first experiment, we evaluated cereal rye seeding rates within no-till soybean production at two Mid-Atlantic locations. We hypothesized that increasing cereal rye seeding rate would decrease winter- and summer- annual weed population densities and the proportion of large individuals within populations at the time of postemergence applications. In our second experiment, we evaluated the potential for delayed cover crop termination (i.e., planting green) to facilitate reduced use of soil-applied residual (PRE) herbicides in comparison to standard cover crop termination (14 d pre-plant) and herbicide management (2-pass program with residuals) tactics within a long-term cropping systems study in Pennsylvania. We hypothesized that use of planting green tactics without soil-applied residual herbicides (PRE), would result in similar (1) summer annual weed population densities and heights at the time of post-emergence application, (2) total peak season weed biomass, and (3) soybean yield when

compared to standard cover crop termination practices in combination with soil-applied, pre-emergent herbicide programs.

Materials and Methods

Cereal rye seeding rate experiment

Field experiments were conducted at the Pennsylvania State University Russell E. Larson Agricultural Research Center (RELARC) near Rock Springs, PA (40°42'N, 77°57'W), the Southeast Agricultural Research and Extension Center (SEAREC) near Landisville, PA (40°07'N, 76°25'W), and the University of Delaware's Research and Education Center (UDREC) near Georgetown, DE (38.64°N, 75.46°W). The experiment was conducted in the 2018-2019 growing season at RELARC and UDREC and in the 2019-2020 growing season at all locations for a total of five site years. The experimental sites differed in soil texture, including Hagerstown silt loam at RELARC, Duffield silt loam soil at SEARC, and Hammonton loamy sand soil at UDREC. Pennsylvania sites were established in the fall following a soybean crop with high infestations of horseweed (*Erigeron canadensis*).

Experimental design and field operations

A single-factor, randomized complete block design with four replications was used to evaluate cereal rye seeding rates, including 0, 51, 101, 135 kg ha⁻¹ at PA locations. This seeding rate gradient includes lower rates commonly used by growers and higher rates thought to optimize weed suppression potential. Due to frequent N limitation in coarse soils, the DE location evaluated cereal rye seeding rate treatments under alternative N fertility levels using a two-factor, randomized complete block design and four replications. The N fertility treatment included 0 kg N ha⁻¹ and 34 kg N ha⁻¹ applied prior to cereal rye seeding.

Cereal rye was no-till drilled using 19-cm row spacing in late September through early November depending on location (**Table 2-1**). Dicamba-resistant soybean (*Glycine max* (L.) Merr.) were planted at each location using a rate of 371,000 seeds ha⁻¹ and 76-cm row spacing with a no-till planter at the cereal rye heading stage (Zadoks 50 - 59; **Table 2-1**). Cereal rye was roll-crimped at planting with ZRX integrated rollers (Dawn Equipment, Sycamore, IL) and

double-disk row-cleaners at PA locations. Cereal rye was not rolled at planting and row-cleaners were not used in DE. A pre-plant burndown application of glyphosate (1.26 kg ae ha⁻¹) + dicamba (0.56 kg ae ha⁻¹) was applied using a carrier volume of 185 L ha⁻¹ to the entire field with a tractor-mounted sprayer within 1 d after soybean planting. At the V4 soybean growth stage, a postemergence application of glyphosate (1.26 kg ae ha⁻¹) + dicamba (0.56 kg ae ha⁻¹) was applied to provide postemergence control.

Table 2-1. Cereal rye management timings and growing degree days across all site-years. Growing degree days were calculated with the base temperature set at 4.4°C (Mirsky et al., 2011).

Location	Growing Season	Cereal rye management and environmental conditions			
		Seeding date	Termination date	Fall GDD [†]	Spring GDD [†]
Rock Springs, PA	2018-2019	September 29, 2018	May 16, 2019	294	400
Rock Springs, PA	2019-2020	October 2, 2019	May 21, 2020	263	367
Landisville, PA	2019-2020	November 1, 2019	May 5, 2020	43	371
Georgetown, DE	2018-2019	October 17, 2018	May 9, 2019	511	693
Georgetown, DE	2019-2020	October 30, 2019	May 20, 2020	192	765

[†]GDD = cumulative growing degree days; Fall = seeding to Dec 31; Spring = Jan 1 to termination

At PA locations, artificial seedbanks of large crabgrass (*Digitaria sanguinalis*), redroot pigweed (*Amaranthus retroflexus*), and common lambsquarters (*Chenopodium album*) were established in 1 m² microplots in the middle of each plot after drilling cereal rye each fall, using seeding rates of 200, 800, and 400 seeds m⁻², respectively. Endemic weed populations were used to evaluate treatment effects on summer annual weed species of interest at the DE location.

Data collection and analysis

Aboveground biomass of cereal rye and weeds was collected in two randomly placed 0.25 m² quadrats within each plot 3-5 days prior to soybean planting. At PA locations, horseweed population density and the height of up to 40 random horseweed plants were recorded prior to biomass sampling within quadrats. Summer annual weed densities, heights, and biomass were recorded 5-6 weeks after soybean planting (WAP) prior to postemergence applications. At the DE location, summer annual weed density was collected each year and biomass was collected in 2018-2019. Aboveground biomass samples were separated by plant species in the laboratory, oven dried at 65°C for 10 days, and weighed. Soybean yields were evaluated using a two-row small plot harvester and are reported at 13.5% moisture.

All statistical analyses were conducted using computing package R (R Core Team, 2019). ANOVA was used to test for differences in cereal rye biomass, weed response variables, and grain yield by location. Pennsylvania models were fit using cereal rye seeding rate as a fixed effect and block nested in site year as random effects. Delaware models were fit using cereal rye seeding rate, fertility, and their interaction as fixed effects and block nested in site year as random effects. Horseweed and winter- and summer-annual weed densities (plants m⁻²) were analyzed with generalized linear mixed effect models using a negative binomial distribution in the *lme4* package (Bates et al., 2016). All other metrics were modeled using linear mixed-effect models in the *nlme* package (Pinheiro et al., 2019). All weed biomass metrics (kg ha⁻¹) were log transformed to achieve normality. Pairwise comparisons of the least-square means were obtained using the *emmeans* package (Lenth, 2020). The *cld* function in the *multcomp* package was used to test for differences between treatments using the *Tukey* procedure (Hothorn et al., 2008). Back-transformed means are presented in the results.

Reduced-herbicide input experiment

A field experiment was conducted at the Pennsylvania State University Russell E. Larson Agricultural Research Center (RELARC) near Rock Springs, PA (40°42'N, 77°57'W) within a long-term dairy cropping systems experiment and replicated for three growing seasons (2019-2021).

Experimental design and field operations

The experiment was imposed during the soybean phase of a 6-yr dairy rotation using a single-factor, paired comparison imposed in split-plots across four replicate blocks. The treatments included a standard cover crop termination (14 - 21 d pre-plant) and herbicide program (pre-plant burndown + preemergence residual + postemergence) compared to delayed cover crop termination (0 d post-plant) and reduced herbicide inputs (reduced pre-plant inputs and exclusion of preemergence residuals; **Table 2-2**). At the postemergence application (5-6 WAP), an IPM approach was employed by scouting weeds and adjusting the herbicide program accordingly. Use of additional herbicide inputs was driven by glyphosate-resistant horseweed abundance (**Table 2-2**). Due to variable weather conditions across years, cereal rye was

terminated 21 d pre-plant in 2019 and 2021 growing seasons and 14 d pre-plant in the 2020 growing season within the standard treatment (**Table 2-3**).

Cereal rye was established each fall with a no-till drill (Great Plains, Salina, KS 67401) using a 135 kg ha⁻¹ seeding rate in both treatments (**Table 2-3**). Soybean (*Glycine max* (L.) Merr.) were planted using a John Deere 1720 MaxEmerge no-till planter (Deere & Company, Moline, IL) equipped with a ZRX integrated roller system (Dawn Equipment, Sycamore, IL) at a rate of 371,000 seeds ha⁻¹ in 76-cm-wide rows (**Table 2-3**). In order to isolate the effect of delayed cover crop termination on suppression of summer annual weeds, artificial weed seedbanks of 400 common lambsquarters (*Chenopodium album*) seeds, 800 redroot pigweed (*Amaranthus retroflexus*) seeds, and 200 large crabgrass (*Digitaria sanguinalis*) seeds were established in a 1 m² microplot within each plot and were excluded from the preemergence herbicide application.

Table 2-2. Herbicide inputs across treatments and years.

Herbicide inputs	Standard			Planting Green		
	2019	2020	2021	2019	2020	2021
<i>Cover crop termination and burndown</i>						
glyphosate (1.26 kg ae ha ⁻¹)	X	X	X	X	X	X
2-4,D ester (0.53 kg ae ha ⁻¹)	X	X	X			
<i>Preemergence soil applied residual</i>						
flumioxazin (0.09 kg ai ha ⁻¹)	X	X	X			
pyroxasulfone (0.11 kg ai ha ⁻¹)	X	X	X			
<i>Postemergence (5-6 WAP)</i>						
glyphosate (1.73 kg ae ha ⁻¹)	X	X	X	X	X	X
cloransulam-methyl (0.04 kg ai ha ⁻¹)		X			X	
glufosinate-ammonium (0.66 kg ai ha ⁻¹)						X
<i>Total number of inputs</i>	5	6	5	2	3	3

Table 2-3. Agronomic management dates, growing degree days, total monthly precipitation, and average monthly temperature in each growing season. Growing degree days were calculated with the base temperature set at 4.4°C (Mirsky et al., 2011).

Field operation	2018-2019	2019-2020	2020-2021
Cereal rye seeding	10/17	9/25	9/23
Cereal rye termination (Standard treatment)	4/30	5/5	4/27
Soybean planting	5/22	5/20	5/18
Cereal rye termination (Planting green treatment)	5/22	5/21	5/18
Soybean harvest	10/11	10/23	10/21
Fall GDD ¹	79	358	456
Standard Spring GDD ¹	239	262	252
Planting Green Spring GDD ¹	481	367	435
Planting Green GDD (difference relative to standard)	242	105	183

¹GDD = cumulative growing degree days; Fall = seeding to Dec 31; Spring = Jan 1 to termination

Data collection and statistical analysis

Aboveground cereal rye biomass was collected in two randomly placed 0.25 m² quadrats per split-plot one day prior to cover crop termination. Density and heights of large crabgrass, common lambsquarters, and redroot pigweed were recorded within the artificial weed seedbanks at the V4 soybean growth stage. As a result of field scouting prior to postemergence applications, horseweed density and heights were collected from two randomly placed 0.25 m² quadrats per split-plot in 2020 and 2021. Weed biomass samples were collected from two randomly placed 0.25 m² quadrats in mid to late August in each year to evaluate season-long weed control levels. All biomass samples were oven dried at 65°C for 10 days and weighed. Soil volumetric water content (VWC; %) was measured weekly for 14 weeks beginning at soybean planting using a Campbell Scientific HydroSense II soil moisture probe (Campbell Scientific, Inc., Logan, UT) at 7.62 cm depth in one random interrow location per plot. Soybean yields were evaluated by harvesting the middle two rows of each plot with a small plot harvester and correcting moisture to 13.5%.

All statistical analyses were conducted using R v. 3.6.1 (R Core Team, 2019). Horseweed and summer annual weed densities were analyzed with generalized linear mixed effect models using a negative binomial distribution in the *lme4* package (Bates et al., 2016). Cereal rye biomass, weed height data, VWC, and grain yield were analyzed using linear mixed effect models in the *nlme* package (Pinheiro et al., 2019). For each of these response variables, mixed-

effects models were fit using management tactic (standard vs. planting green), site year, and their interaction as fixed effects and block as a random effect. In order to assess treatment effects on weed heights at the postemergence application timing, data were expressed as the proportion of total density that exceeded 10 cm in height. Horseweed height data were subjected to an arcsine transformation to achieve normality. A repeated measures ANOVA was used to test the effect of sampling date by year on the difference between the VWC in the planting green treatment from the standard termination timing. Each year's model was fit using date as a fixed effect and date nested in plot as random effects. VWC data were expressed as the difference relative to the standard treatment within each main plot. The *emmeans* package was used to obtain least-square means (Lenth, 2020) and the *cld* function in the *multcomp* package was used to test for differences between treatments with pairwise comparisons of the least-square means using the *Tukey* procedure (Hothorn et al., 2008). Back-transformed means are presented in results.

Results

Cereal rye seeding rate experiment results

Our results did not support the hypothesis that increasing cereal rye seeding rates would decrease weed population densities, biomass, and the proportion of large individuals within populations at the time of pre-plant and postemergence applications. Notably, cereal rye seeding rate had no effect ($P > 0.05$) on cereal rye biomass in PA and DE, and no differences in winter annual weed biomass or density were found in pairwise comparisons of alternative seeding rates (**Table 2-4; Table 2-5**). However, each cereal rye seeding rate significantly reduced winter annual weed biomass or density ($P < 0.001$) compared with the control at the pre-plant herbicide application timing (**Table 2-4; Table 2-5**), including horseweed densities ($P < 0.001$), which were measured at the RELARC location each year (**Figure 2-1**). Averaged across treatments, cereal rye reduced winter annual weed biomass 85% to 92% and horseweed density 65% to 75% compared to the control. Similar results were observed at DE, where cereal rye treatments decreased winter annual weed density 42% to 59% just prior to the pre-plant application timing. Cereal rye seeding rates did not significantly ($P > 0.05$) influence the proportion of horseweed individuals over 10 cm in height at the PA location.

A significant ($P < 0.01$) seeding rate effect was observed at the postemergence application timing at PA locations (**Table 2-4**). Each cereal rye seeding rate reduced summer annual weed density compared to the control by approximately 51% to 57%. However, no significant differences in summer annual weed density were detected between 51 kg ha⁻¹ and 135 kg ha⁻¹ seeding rates. Across treatments, less than 1% of summer annual weeds were over 10 cm in PA site-years at the postemergence application timing.

At the DE location, cereal rye seeding rate ($P < 0.01$) and soil fertility ($P < 0.05$) affected summer annual weed density, but no interaction was observed (**Table 2-5**). Fertility treatment, 34kg N ha⁻¹, reduced summer annual weed density compared to 0 kg N ha⁻¹. Averaged across fertility treatments, summer annual weed densities decreased by 45% to 48% across the range of seeding rates compared to the control. There was no significant treatment effect on the proportion of summer annuals over 10 cm in height and total summer annual weed biomass in DE site years. However, summer annual weed biomass significantly differed by species ($P < 0.001$). Seeding rate had no significant effect on summer annual weed biomass. Common ragweed had significantly lower weed biomass compared to morningglory and palmer amaranth but morningglory and palmer amaranth did not differ from each other (**Figure 2-2**). No treatment effects were observed on soybean yield at both locations (**Table 2-4; Table 2-5**).

Table 2-4. Effects of cereal rye seeding rates on cereal rye and winter annual weed biomass at planting, summer annual weed density 4-5 weeks after soybean planting, and soybean yield. Data are means averaged across Pennsylvania site years (n = 3).

Cereal rye seeding rate	Cereal rye biomass	Winter annual weed biomass	Summer annual weed density	Soybean yield
kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹	plt m ⁻²	kg ha ⁻¹
0	---	701 a	54 a	2,962
51	3,672	102 b	26 b	3,112
101	4,094	53 b	23 b	2,975
135	3,700	80 b	24 b	2,988
ANOVA	----- P-value. -----			
Seeding rate	ns	***	**	ns

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = non-significant

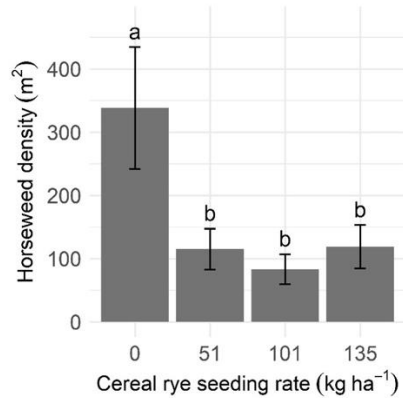


Figure 2-1. Effect of cereal rye seeding rates on mean horseweed density at cover crop termination at Rock Springs, PA locations. Data are treatment means (± 1 SE) averaged across two site-years (2019-2020).

Table 2-5. Effects of cereal rye seeding rates on cereal rye biomass, winter- and summer-annual weed densities 4-5 weeks after planting, and soybean yield. Data are means averaged across the Delaware site years ($n = 2$).

Cereal rye seeding rate	Cereal rye biomass	Winter annual weed density [†]	Summer annual weed density	Soybean yield
kg ha ⁻¹	kg ha ⁻¹	plt m ⁻²	plt m ⁻²	kg ha ⁻¹
0	-	39 a	45 a	2,095
51	2,082	22 b	23 b	2,583
101	2,485	20 b	25 b	2,611
135	2,355	16 b	24 b	2,399

ANOVA	P-value.			
Seeding rate	ns	***	**	ns
Fertility	ns	ns	*	ns
S x F	ns	ns	ns	ns

[†]Only 2020 site year;; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = non-significant

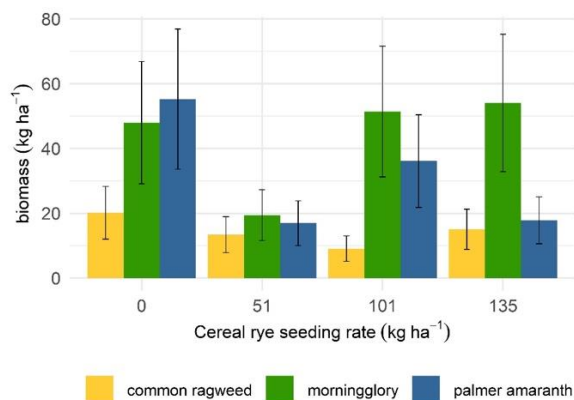


Figure 2-2. Summer annual weed biomass by species across cereal rye seeding rates in Delaware 2019 site-year.

Reduced-herbicide experiment results

Our results showed partial support for the hypothesis that the combination of delayed cover crop termination (i.e., planting green) and reduced herbicide inputs would result in similar weed control performance and soybean yield compared to the standard cover crop termination and herbicide programs. A significant interaction between termination timing and year ($P < 0.001$) was observed in analysis of cereal rye biomass production (**Figure 2-3**). Planting green treatments resulted in significantly more cereal rye biomass compared to the standard treatment each year but differed in the magnitude of the response. We observed a 63% increase in cereal rye biomass production within planting green treatments in 2019, but only a 22% and 33% increase in 2020 and 2021, respectively. Planting green increased GDD by 242, 105, and 183 days in 2019, 2020, and 2021, respectively, which was partially driven by the differences in termination timings and may have attributed to observed differences in the magnitude of responses across years (**Table 2-3**). At the postemergence application timing, the interaction between termination timing and year ($P < 0.01$) had significant effects on biomass of cereal rye residue on the surface. Cereal rye surface residues did not differ across treatments in 2020 and 2021, but planting green increased cereal rye surface residues by 90% at this timing in 2019.

Variation in the selection of postemergence herbicide programs was driven by abundance of endemic horseweed populations (**Table 2-2**). In 2019, no additional active ingredients were tank-mixed with glyphosate programs due to the absence of horseweed, whereas cloransulam-

methyl was applied in 2020 to target horseweed in dicamba-tolerant soybean (Xtend®) and glufosinate was applied in 2021 in dicamba/glufosinate- tolerant soybean (XtendFlex®). In the latter two years, horseweed density and proportion of large individuals within the population significantly differed ($P < 0.001$) between termination timing treatments at the postemergence timing (**Table 2-6**). The standard treatment resulted in significantly lower horseweed densities compared to planting green treatments, which can be attributed, in part, to the combination of effective sites-of-action used for postemergence horseweed control at the pre-plant burndown application timing and soil-applied residual products applied at planting (**Table 2-6**). At the postemergence application timing, there were no horseweed individuals greater than 10 cm in height in the standard treatments across both years, whereas 17% and 62% of horseweed individuals were over 10 cm in 2020 and 2021, respectively, in planting green treatments (**Table 2-6**). In residual-herbicide exclusion microplots, no significant treatment effects were observed on summer annual weed density and proportion of large individuals at the time of postemergence application (**Table 2-6**).

Due to adequate weed control efficacy of horseweed and other endemic summer annual species at the postemergence application timing, no treatment effect on peak season weed biomass ($< 4 \text{ kg ha}^{-1}$) was detected. At the time of postemergence application, termination timing ($P < 0.01$) and year ($P < 0.0001$) had significant effects on soybean biomass but there was not a significant interaction. The standard cover crop termination significantly reduced soybean biomass in 2019 and 2020, which was likely due to herbicide injury as a result of heavy rain events causing flumioxazin to splash on soybean leaves. Year ($P < 0.0001$) had a significant effect on soybean populations, but termination timing and the interaction between termination timing and year did not. Termination timing ($P < 0.05$), year ($P < 0.001$), and their interaction ($P < 0.05$) had significant effects on soybean yield. In 2019 and 2021, soybean yield did not differ across treatments (**Figure 2-4**). However, planting green significantly reduced soybean yield by 27% in 2020 compared to the standard treatment. VWC was significantly lower in planting green treatments compared to the standard at multiple early season dates in May 2021 and a late season date in August 2019 ($P < 0.05$; **Figure 2-5**). VWC was significantly higher in planting green treatments compared to the standard at multiple early- to mid-season dates in June and July 2021

($P < 0.05$; **Figure 2-5**). In 2020, VWC decreased across both termination timing treatments due to low precipitation throughout the growing season (**Figure 2-6**). However, trends show planting green reduced VWC at early- to mid-season in 2020 compared to the standard termination, but our results were not statistically significant (**Figure 2-5**).

Table 2-6. Treatment and site-year effects on horseweed and summer annual weed density and proportion of large individuals (> 10 cm hgt) at the time of postemergence applications.

Treatment	Year	Horseweed [†]		Summer annual weeds	
		density plt m ⁻²	> 10 cm hgt %	density plt m ⁻²	> 10 cm hgt %
Standard	2019	-	-	7	34
Planting green	2019	-	-	7	40
Standard	2020	1	0	8	05
Planting green	2020	22*	17*	9	01
Standard	2021	0	0	9	31
Planting green	2021	6*	62*	9	26
ANOVA ¹		-----P-value-----			
Treatment (T)		***	***	ns	ns
Year (Y)		*	**	ns	***
T × Y		ns	**	ns	ns

[†]Only 2020 and 2021 included in analysis; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, *ns* = non-significant

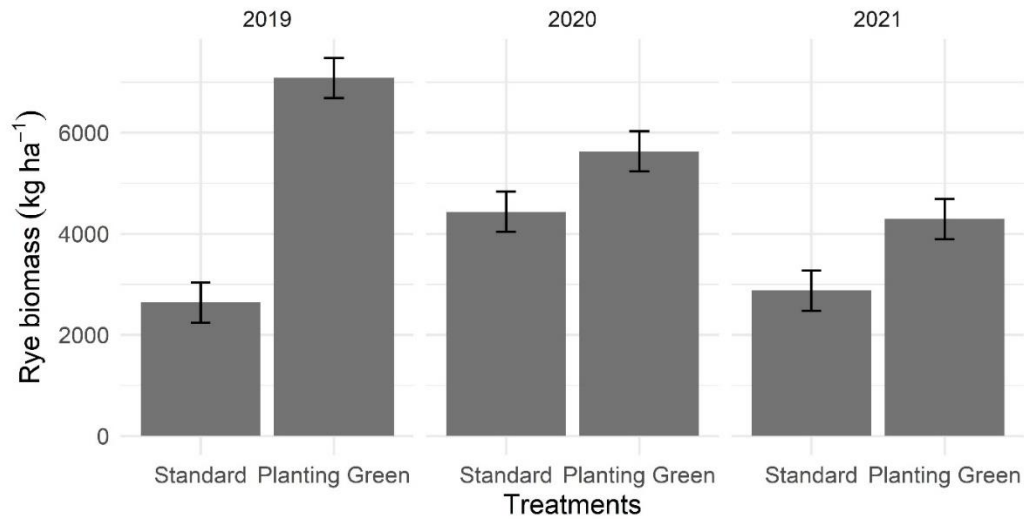


Figure 2-3. The effects of termination timing (standard vs. planting green) on mean cereal rye biomass across three growing seasons (2019-2021). Standard termination data was collected 14-21d prior to soybean planting. Planting green data was collected at soybean planting at the cereal rye heading stage (Zadoks 50-59). Data are treatment means (± 1 SE) averaged across plots.

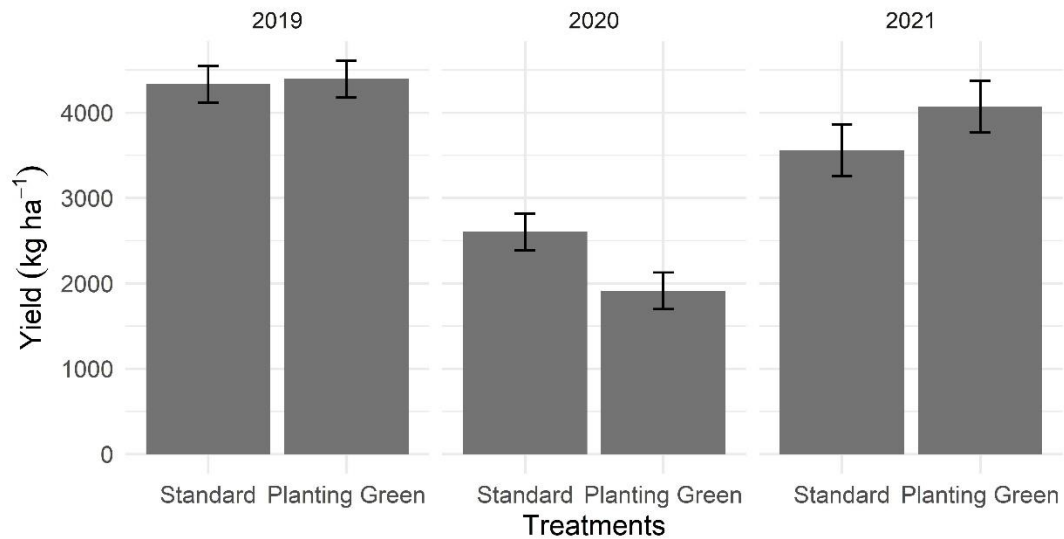


Figure 2-4. The effects of termination timing (standard vs. planting green) on mean soybean yield across three growing seasons (2019-2021). Cereal rye was terminated 14-21d prior to soybean planting and a standard herbicide program was used in the standard treatment. Cereal rye was terminated at soybean planting and reduced herbicide input program was used in the planting green treatment. Data are treatment means (± 1 SE) averaged across plots.

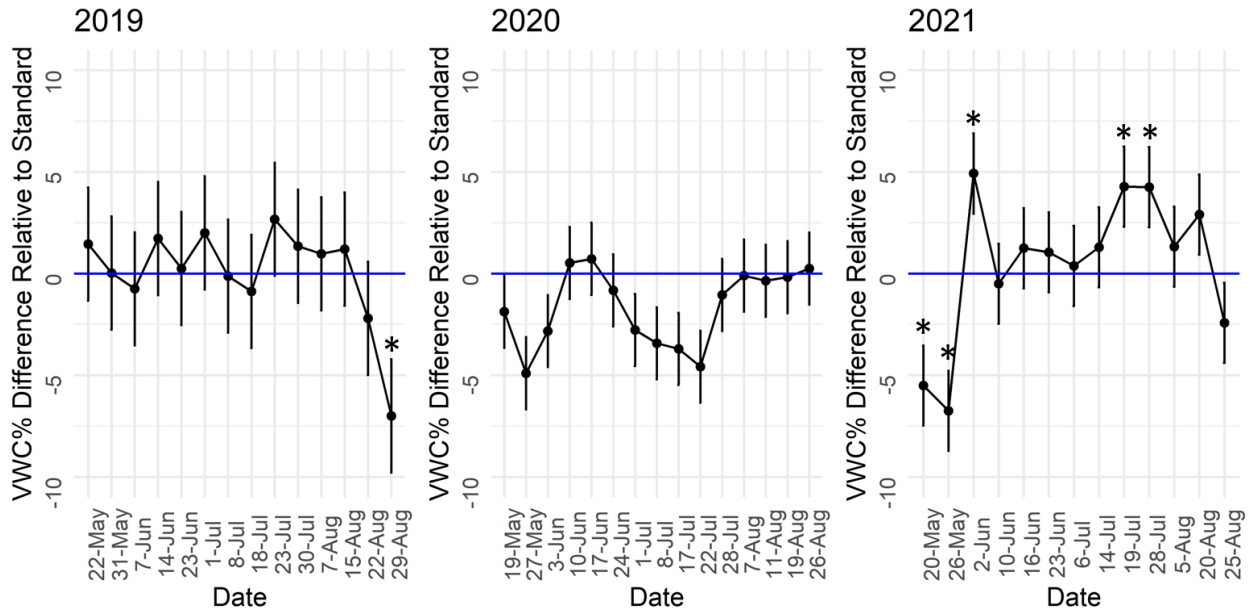


Figure 2-5. The effects of planting green on soil volumetric water content (%) relative to standard termination timing across three growing seasons (2019-2021). Data are treatment means (± 1 SE) averaged across plots. * Indicates significant planting green VWC differences relative to standard termination timing.

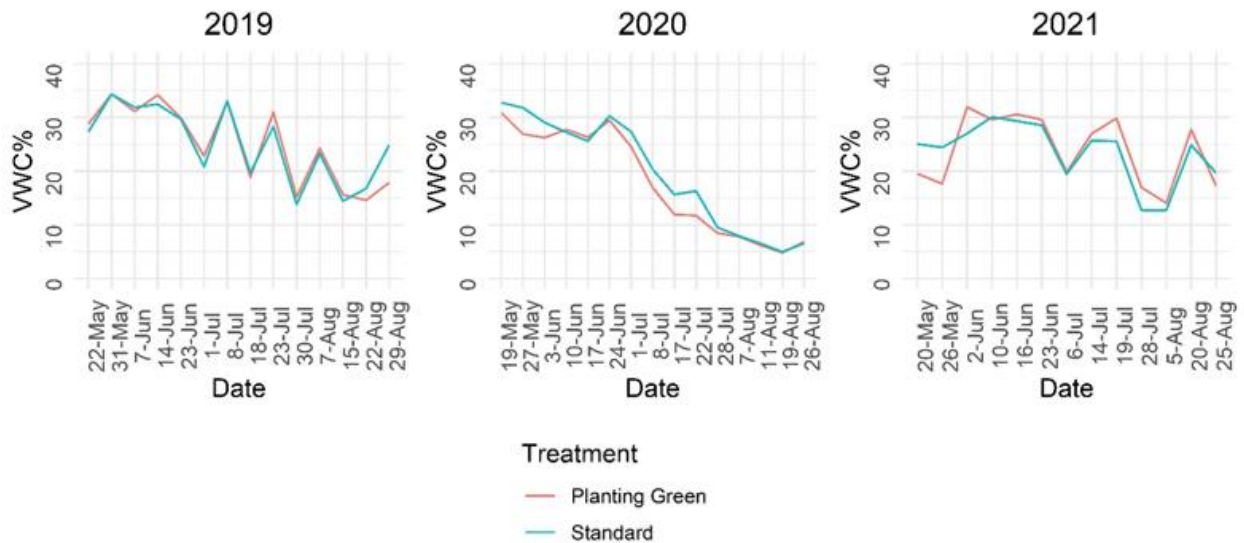


Figure 2-6. Mean soil volumetric water content (%) in planting green and standard termination timing treatments across three growing seasons (2019 - 2021).

Table 2-7. Total monthly precipitation and average monthly temperature in each growing season and monthly normal precipitation and temperature (1981 – 2010) at Rock Springs, PA.

Month	Precipitation				Temperature			
	2019	2020	2021	Monthly normal	2019	2020	2021	Monthly normal
	----- mm -----				----- °C -----			
May	158.0	91.0	116.1	92.5	16.7	14.0	14.7	15.4
June	91.7	125.5	109.7	103.9	19.5	20.6	21.2	20.1
July	63.8	35.1	146.6	96.3	23.6	25.0	22.8	22.3
August	67.1	51.6	123.7	105.7	21.5	23.5	23.5	21.3
September	47.5	57.7	223.8	100.3	18.7	17.3	18.8	17.3
October	114.3	83.9	89.0	87.9	12.2	11.9	15.2	11.1

Discussion

Cereal rye seeding rate experiment

Our results indicate that cereal rye seeding rates have limited effects on winter- and summer- annual weed recruitment in the context of planting green tactics. The lack of weed suppression differences are likely due to the lack of seeding rate effects on cereal rye biomass accumulation when seeding rates ranged 51 to 135 kg ha⁻¹. Mirsky et al. (2017) found that to maximize cereal rye biomass, an application of 72 kg N ha⁻¹ in addition to soil residual N was necessary. At anthesis, cereal rye without N fertilizer produced 75% of the biomass of cereal rye with 150 kg N ha⁻¹ applied (Steven B. Mirsky et al., 2017). In our experiment, we found an average of 89% of winter annual and 55% of summer annual weed suppression across seeding rates that produced 3,700 to 4,000 kg ha⁻¹ of biomass. An average of 50% and 47% of winter annual and summer annual weed suppression, respectively, was achieved across seeding rates that produced 2,000 to 2,500 kg ha⁻¹ of biomass. Our results are consistent with previous studies that have found similar weed suppression benefits of cover crops (Beam et al., 2021; Desimini et al., 2020; Pittman et al., 2019; Schramski et al., 2021).

Our results showed an average of 70% reduction in horseweed density within cereal rye treatment at the time of pre-plant herbicide applications. This can be viewed as a resistance management benefit, by reducing the selection pressure on currently effective modes of action

used for horseweed control at a pre-plant application timing, such as 2,4-D ester, dicamba, or saflufenacil. Our results also indicate that lower and more economical cereal rye seeding rates (51 kg ha⁻¹) can provide weed suppression benefits equal to higher seeding rates. Previous studies have found that growing degree days and high plant-available nitrogen are the primary drivers of cereal rye biomass production (Essman et al., 2020; Feyereisen et al., 2006; Mirsky et al., 2017; Reed et al., 2019; Schramski et al., 2021; Vollmer et al., 2020). Considering that our experiment was seeded at optimal dates for cereal rye, increasing seeding rates may still be a tactic for increasing cereal rye biomass production when seeded at later dates or under nitrogen-limited fall growing conditions. While residue management via integrated roll-crimpers and row-cleaners was implemented in PA site-years, no modifications were used in DE. Cover crop surface residue management remains a potential limiting factor when planting green, but soybean yield was not influenced by cereal rye residues in our experiments.

Reduced-herbicide experiment

Our experimental results indicate that increased weed suppression via delayed cover crop termination timing (i.e., planting green) in combination with reduced herbicide inputs can result in similar weed control levels compared to standard cover crop termination and herbicide programs. These results are likely weed species specific and may be limited to small-seed summer annual broadleaf or grass species. In supporting research, we have found that cereal rye biomass of 3,360 – 10,080 kg ha⁻¹ had minimal effect on the establishment rates of large seeded species like burcucumber (*Sicyos angulatus*) and common morningglory (*Ipomoea purpurea*) while establishment of small seeded species like palmer amaranth (*Amaranthus palmeri*) and common ragweed (*Ambrosia artemisiifolia*) was substantially reduced (Ficks et al., 2021). In addition, planting green tactics will likely not fully control herbicide-resistant weed populations that have extended emergence periods, such as horseweed and *Amaranthus* species, so integration of herbicide programs that include effective sites-of-action is critical to maintaining control of these populations. Our glyphosate-resistant horseweed population results demonstrate the importance of effective sites-of-action for pre-plant burndown and soil-residual herbicide applications. Overall, an IWM approach with planting green tactics and a standard cover crop termination and herbicide program both maintained crop protection goals associated with weed control.

Our results indicate that delaying cover crop termination via planting green tactics can consistently increase cover crop biomass compared to standard termination practices. Greater biomass accumulation results from additional growing degree days between termination timings (**Table 2-3**). Earlier seeding dates and higher plant-available nitrogen in the fall could further increase biomass production potential and weed suppressive benefits of planting green tactics (Essman et al., 2020; Feyereisen et al., 2006; Mirsky et al., 2017; Reed et al., 2019; Schramski et al., 2021; Vollmer et al., 2020).

Our soybean yield results indicate a potential yield tradeoff when planting green in some years. Soybean yield reductions in the planting green treatment in 2020 can be attributed, in part, to observed soil moisture patterns. Planting green likely creates soil moisture deficits early in the season but may conserve soil moisture later in the season if residue persists. Early season soil moisture deficits can be attributed to cover crops growing longer and actively using soil moisture until after termination in planting green systems (Mirsky et al., 2011; Reed et al., 2019). Consequently, delayed cover crop termination may hasten or expand soybean planting windows during wet springs, but continued loss of soil moisture when cover crop termination is delayed may be detrimental for achieving optimum seed depth and crop germination during a dry spring (Reed et al., 2019). Given our soybean population results, soil moisture deficits at planting in the planting green treatment likely did not affect soybean stand establishment. Soil moisture conservation after cover crop termination is likely due to increased cover crop surface residue biomass when planting green (Reed et al., 2019). However, throughout most of the 2020 growing season, soil moisture deficits in planting green relative to the standard termination treatment continued through the growing season. In 2020, precipitation was lower in May, July, August, and October compared to 2019 and 2021 growing seasons (**Table 2-4**). Since precipitation was low throughout the 2020 growing season, little to no moisture was returned to the soil so a soil moisture conservation benefit of planting green was not realized. Prolonged soil moisture deficits in planting green can be detrimental to crop reproductive development causing potential yield reductions. Our 2019 and 2021 results are consistent with Reed et al. (2019) that found delayed cover crop termination tactics reduced soil moisture at planting but increased soil moisture a few weeks after planting compared to terminating the cover crop prior to planting.

In our study, planting green tactics reduced herbicide inputs (no. of active ingredients) by 50% and still maintained similar levels of weed control. Reducing herbicide inputs in combination with planting green tactics will likely be more sustainable in a diversified cropping system, where our experiment took place, compared to simplified crop rotations. Weed suppression levels observed in our reduced-herbicide input treatments should be viewed in the context of relatively low weed seedbank densities typical of long-term dairy cropping systems (Nichols et al., 2015; Pakeman et al., 2020; Schwartz-Lazaro & Copes, 2019; Snyder et al., 2016; Summers et al., 2021). Planting green may not be as effective in systems with higher weed seedbank densities and weed communities containing large seeded species. Our results demonstrate that herbicide resistant weed populations require comprehensive herbicide programs when planting green tactics are utilized. Planting green effects associated with water availability and the resulting impact on soybean yields should be of concern for many growers, requiring careful consideration of herbicide input savings and yield tradeoffs when utilizing planting green tactics for weed suppression services.

Management Implications

Our experimental results indicate opportunities to reduce either cover crop seeding rates or herbicide inputs while utilizing planting green tactics, but crop performance may be compromised under certain agronomic conditions. Cereal rye seeding rates may be reduced to 51 kg ha⁻¹ and still achieve similar weed suppression as higher seeding rates when planting green. Since other agronomic and environmental factors are known to effect cover crop biomass, seeding rate input savings may likely be realized when cereal rye is seeded at optimal dates and plant-available nitrogen is not a limiting factor. Opportunities to replace residual herbicides when planting green may create cost-saving opportunities when herbicide resistant weed populations are not present. However, our results indicate the potential for soybean yield penalties when spring precipitation is low. Planting green is not recommended in dry springs. Dry soil conditions may cause problems with planting depth, germination, and limit moisture for the developing crop (Reed et al., 2019).

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Chapter 3

Weed seed mass affects seedling establishment and resource allocation patterns across a cereal rye surface residue gradient

Knowledge of weed population- and community- level responses to the integration of cover crop surface residues (CCSRs) into a weed management program is vital to understanding their value in no-till field crop production systems. Given that seedlings are dependent on their seed resources prior to establishment, the seedling's fitness advantage to overcome CCSR conditions is a function of seed mass in which larger seeds tend to have greater available resources to facilitate survival strategies. We investigated the ecological implications CCSR have on seedlings of species across a seed mass gradient by answering the following questions: (1) Do large-seeded species improve seedling establishment metrics under increasing CCSR biomass compared to small-seeded species? (2) Do seedlings divert resources to hypocotyl tissue at a cost to other organs under increasing CCSR biomass? A greenhouse experiment was conducted in the fall of 2020 to evaluate 8 weed species and 2 crop species' responses to cereal rye mulch treatments of 0, 3,360, 6,720, and 10,080 kg ha⁻¹. Our results indicate that large-seeded species improved seedling establishment metrics under increasing CCSR biomass. Resources were diverted to hypocotyl tissue and length under increasing CCSR biomass, but CCSR had no significant effect on other organs. Our results suggest that increasing CCSR biomass has positive weed management implications for small-seeded species, but control of large-seeded species may not be feasible. However, resource allocation patterns induced by CCSR will likely lead to greater susceptibility to other potential hazards across the seed mass gradient.

Introduction

Cover crop surface residues (CCSRs) are increasingly adopted as a weed suppression tactic in conventional and organic no-till field crop production systems (CTIC, 2020). Previous field studies have established a negative relationship between the mass of CCSR and weed density or biomass (Mohler and Teasdale, 1993; Teasdale and Mohler, 1993). More recent efforts have been made to identify biomass production levels of cereal rye (*Secale cereale*, L.), a common species used in CCSR systems, that provide meaningful weed suppression benefits. For example, Nichols et al. (2020) estimated that 5,000 kg ha⁻¹ of cereal rye surface residue is needed

in the Midwestern U.S. to reduce summer annual weed biomass by 75%. Studies focusing on organic no-till production indicate that higher CCSR biomass thresholds, ranging from 6,000 to 9,000 kg ha⁻¹, are needed to provide acceptable levels of weed suppression (Mirsky et al., 2013). However, weed control levels from CCSRs can be highly variable and depend on the weed species present. Greater understanding of the interaction between weed seed traits and resource allocation patterns of common weed species, and how these factors influence establishment within CCSRs, may help forecast changes in weed seedbank dynamics and community shifts in systems utilizing CCSRs.

Current understanding of weed suppression via CCSRs has primarily used weed population data censused after the seedling establishment life-cycle transition. Weed seedling establishment is a critical phenological event during which a seedling transitions from relying on nonrenewable seed reserves to photosynthetic autotropism (Forcella et al., 2000). Weed population densities measured in CCSRs represent the product of germination and seedling survival rates. Therefore, reduced weed densities in response to CCSRs may result from either (1) failure to germinate due to the attenuation of germination cues, or (2) fatal germination, in which seeds germinate but do not survive to seedling establishment. CCSRs influence weed seed germination via indirect effects on factors that modify or terminate seed dormancy and initiate seed germination, including light flux density and quality, temperature amplitude, soil nitrate levels, and soil moisture retention (Teasdale & Mohler, 1993). Once germination occurs, CCSRs influence seedling establishment rates via physical interference that requires resource allocation to shoot elongation until it emerges through the residue mulch layer and establishes as an autotrophic plant (Bruce et al., 2006; Kitajima and Fenner, 2000; Ganade and Westoby, 1999; Leishman and Westoby, 1994).

Weed life cycles are particularly vulnerable in the transition between the germination and seedling establishment phase because the seedling is dependent on seed resources for survival (Leishman et al., 2000; Fenner & Thompson, 2005). Germinated seedlings must tolerate low light conditions, phytotoxin exudates, and altered soil moisture and temperature within the residue mulch, all of which are exacerbated at higher levels of residue biomass (Mirsky et al., 2013). Consequently, CCSR systems that maximize biomass production may create a strong filter on weed community assembly, where fitness is a function of seed mass. Though weed

species vary considerably in seed mass, they are most often operationally defined as either small- or large- seeded using agronomic crop seed mass a relative measure (Mohler, 1996). Weed species with average seed mass that are one to three orders of magnitude smaller in than agronomic crops, such as maize (*Zea mays* L.) and soyabean (*Glycine max* L.), are typically classified as small-seeded, whereas species that are less than an order of magnitude smaller than crops are classified as large-seeded. Such a distinction provides a starting pointing for forecasting population processes (i.e., emergence rates), weed-crop competition, and other evolutionary-based life-history tradeoffs. For example, large-seeded species tend to have greater seed reserves and larger initial seedling size, which increase survival under low-light conditions that create carbon deficits during the establishment phase (Ganade and Westoby, 1999; Kidson and Westoby, 2000; Leishman and Westoby, 1994; Westoby et al., 1996). However, small-seeded species have higher relative growth rates, which can confer a fitness advantage over large-seeded species under non-limiting resource conditions in the post-establishment phase (Ganade and Westoby, 1999). In CCSR systems, small-seeded weed species likely have comparatively lower survival rates because fewer resources are available to allocate towards hypocotyl elongation, which is necessary for penetrating the residue mulch layer. Additionally, previous studies have found that small-seeded weed species are more susceptible to allelopathic compounds released from cover crop residues during germination and seedling establishment compared to large-seeded species (Kruidhof et al., 2011; Liebman and Sundberg, 2006; Mohler, 1996). Studies examining the role of seed mass on survival to establishment and resource allocation patterns under surface residues have been limited to forested systems (Green and Juniper, 2004; Leishman and Westoby, 1994; Myers and Kitajima, 2007).

Understanding how variation in seed mass among arable weed species and crops affects seedling establishment rates and resource allocation patterns in CCSR systems can inform the design of multi-tactic strategies for managing weeds at a community level. Toward this end, we conducted a greenhouse experiment to evaluate the effects of CCSRs on seedling establishment and resource allocation of weed and crop species varying in seed mass across a cereal rye surface mulch gradient. Levels of cereal rye mass were selected based on currently recommended and achievable biomass production targets under field conditions in the Mid-Atlantic U.S. region. We expected the seedlings of large-seeded species to have higher seedling establishment and

absolute growth rates (AGRs) compared to the seedlings of the small-seeded species under increasing CCSR levels. We hypothesized that as CCSR mass increases, resource allocation to root mass, leaf mass, and leaf area will decrease due to diversion of resources to hypocotyl elongation. We expected a greater effect on resource allocation in small-seeded species compared to large-seeded species.

Materials and Methods

Experiment Design

A greenhouse experiment was conducted in the fall of 2020 at University Park, PA using a randomized complete block design with a split-plot treatment structure, two experimental runs, and four replications per experimental run. Experimental runs were initiated 7 d apart. Main plot treatments utilized cereal rye to establish a CCSR biomass gradient (0, 3360, 6720, and 10080 kg ha⁻¹). Split-plot treatments include two crop and eight weed species (**Table 3-1**). Maize and soyabean were included because they are primary crops in which CCSRs are utilized in the Mid-Atlantic region. Weed species selection was based on agronomic importance, taxonomic group, and variation in seed mass. Split-plot treatments were randomized within CCSR main plot treatments and the location of main plots on greenhouse benches were randomized within replicate blocks. Experimental units consisted of an individual plant grown within a polyvinyl chloride pot (7.6 cm diameter, 15.2 cm high), which was filled with 3:1 field soil to sand mixture and arranged in a 2 by 6 layout within main plots (**Figure 3-1a**). Each pot was split in half and reattached prior to experimental setup to facilitate root mass harvest. Field soil used for the experiment was collected from a local site without history of grain crop production and was steam-sterilized to terminate weed seeds prior to mixing with sand.

Table 3-1. Taxonomic group and seed mass (mg 100-seed⁻¹) of crop and weed species used in greenhouse experiment.

Common name	Scientific name	Taxonomic group	100-seed mass (mg)	weed:crop seed mass [†]
Palmer amaranth	<i>Amaranthus palmeri</i>	dicotyledon weed	2.6×10^1	0.001
large crabgrass	<i>Digitaria sanguinalis</i>	monocotyledon weed	4.7×10^1	0.002
common ragweed	<i>Ambrosia artemisiifolia</i>	dicotyledon weed	1.7×10^2	0.008
giant foxtail	<i>Setaria faberi</i>	monocotyledon weed	2.4×10^2	0.01
velvetleaf	<i>Abutilon theophrasti</i>	dicotyledon weed	8.9×10^2	0.05
shattercane	<i>Sorghum bicolor</i>	monocotyledon weed	8.9×10^2	0.05
annual momingglory	<i>Ipomoea purpurea</i>	dicotyledon weed	3.4×10^3	0.17
burcucumber	<i>Sicyos angulatus</i>	dicotyledon weed	8.7×10^3	0.44
soyabean	<i>Glycine max</i>	dicotyledon crop	1.7×10^4	---
corn	<i>Zea mays</i>	monocotyledon crop	2.2×10^4	---

[†]100-seed mass (mg) of weed species expressed as a proportion of crop 100-seed mass, using the average of corn and soyabean

Experimental Procedures

Cereal rye was sown at 100 kg ha⁻¹ in the fall of 2019 at the Russell E. Larson Agricultural Experiment Center at Rock Springs, PA, bulk harvested from the field at the heading stage (Feekes 10.5) in May 2020, and then stored in the cooler (4°C) for 5 months until initiation of the greenhouse experiment (Zadoks et al., 1974). CCSR treatments were imposed using fresh cereal rye residue but calculated on a dry weight basis by weighing cooler-stored and oven-dried (65°C) subsamples to establish a fresh to dry weight ratio. Weed species were collected the preceding fall from local populations, cleaned using a series of sieves, and then cold moist stratified for 3 months in the cooler (4°C). In order to exclude the germination phase from the experiment, preliminary germination assays were conducted for each weed and crop species to determine the mean number of days to germination.

To initiate each experimental run, placement of species in the growth chamber was staggered so germination of all species occurred within 48 hrs of each other. Once the radicle emerged from each seed, the germinated seed was placed in its respective pot and date was recorded. Each germinated seed was placed in a furrow large enough to accommodate the seed and radicle, then a thin layer of soil media was placed on top so that the seed was just below the soil surface. As soon as a germinated seed was placed in a pot within a group, a wire basket was placed on top (**Figure 3-1b**), and the respective CCSR treatment was placed inside the basket (**Figure 3-1c**). Supplemental lighting was supplied to allow for approximately 20 to 25 daily

light integrals throughout the duration of the experiment. Irrigation was used for 3 days prior to the start of the experiment and throughout the duration of the experiment to prevent water from becoming a limiting factor.



Figure 3-1. (a) Polyvinyl chloride pots arranged in a 2 by 6 layout within the main plot; (b) Wire basket with 0 kg ha⁻¹ CCSR treatment placed on top of the polyvinyl chloride pots; (c) CCSR inside of the wire basket that is on top of the polyvinyl chloride pots.

Data Collection

Seedling emergence was monitored daily and harvested at establishment. Broad-leaved seedlings were considered established when the second true leaf began to emerge (Bruce et al., 2006). Monocotyledon seedlings were considered established when the second true leaf and second collar region were visible. Experimental units without emerged individuals were inspected 28 days after each experimental start and were classified as either living seedlings that did not emerge above the mulch or as seedling mortality. Harvest date and hypocotyl length of broad-leaved seedlings were recorded for each experimental unit. Hypocotyl length was measured from the soil surface to the base of the cotyledons using 0.01 mm precision calipers (Bruce et al., 2006). Each plant was clipped at the soil surface. Biomass of monocotyledon seedlings was divided into aboveground and belowground components. Biomass of broad-leaved seedlings was divided into hypocotyl, cotyledon, leaf, and root components. Leaf biomass components included petioles. The soil media and roots associated with each harvested seedling were washed through a 2-mm sieve to facilitate belowground biomass collection and reduce the likelihood of root biomass loss. The first true leaf area (TLA) of all seedlings was obtained using a LI-COR Biosciences LI-3100C area meter (LI-COR Biosciences, Lincoln, NE). All biomass components were oven dried at 65°C for 10 days and weighed.

Multiple seedling establishment and resource allocation metrics were calculated to assess the interactive effects of CCSR and seed mass (**Table 3-2**). Seedling establishment metrics included (1) probability of seedling establishment, (2) days to establishment, and (3) absolute growth rate (AGR). Resource allocation patterns were measured by calculating biomass components (shoot, root, leaf, or hypocotyl) relative to total plant biomass (i.e., mass fraction; Poorter et al., 2012; Poorter & Sack, 2012). Specific hypocotyl length (SHL) was expressed as the ratio of hypocotyl elongation length and biomass.

Statistical Analysis

Seedling establishment and resource allocation metrics (**Table 3-2**) were modeled using general or generalized linear mixed models in statistical computing package R (R Core Team, 2019). To test the hypothesis that seed functional traits (i.e., mass) are a predictor of seedling establishment rates across CCSR gradients, seedling establishment and resource allocation metrics were modeled as a function of CCSR, seed mass, and their interaction. To identify differences in species level responses to CCSR gradients, seedling establishment and resource allocation metrics (**Table 3-2**) were also modeled as a function of CCSR by species. Survival to establishment data were pooled across experimental run and modeled using logistic regression with a binomial distribution in the *stats* package (R Core Team, 2019). All other metrics were modeled using linear regression in the *nlme* package (Pinheiro et al., 2019) and included experimental run and block nested within experimental run fit as random effects. The natural logarithm of each species' 100-seed mass (mg) was used in models that included seed mass as a predictor variable. Days to establishment, AGR, TLA, and SHL response variables were log transformed to obtain normality. Model assumptions were visually assessed using plots of fitted versus residual values. Due to low survival rates at high CCSR treatment levels (6720 and 10080 kg ha⁻¹), *Amaranthus palmeri* S. Watson was excluded from additional establishment and resource allocation analyses. Data from the 10,080 kg ha⁻¹ CCSR treatment was excluded from *Digitaria sanguinalis* (L.) Scop., *Ambrosia artemisiifolia* L., *Setaria faberi* Herrm., *Abutilon theophrasti* Medik., and *Sorghum bicolor* (L.) Moench nothosubsp. *Drummondii* (Steud.) de Wet ex Davidse treatments because the probability of survival at this treatment level was less than 0.30 for these species, which resulted in few observations within the 10080 kg ha⁻¹ treatment having a disproportionate weight on slope coefficients. The marginal coefficient of determination

(R^2_m), which describes the proportion of the variance in the response associated with fixed effects only, was calculated for each linear regression model using the *sjstats* package (Lüdtke, 2019; Nakagawa & Schielzeth, 2013). McFadden’s coefficient of determination statistic, which describes the maximum likelihood of the model compared to the null model, was calculated for the logistic regression model using the *DescTools* package (Menard, 2000; Signorell et al., 2021).

Table 3-2. Growth analysis metrics, abbreviation, units, and definitions.

Metrics		Units	Definition
<i>Seedling Establishment</i>			
Probability of establishment	-	0-1	Probability of a seedling to survive to establishment.
Days to establishment	-	day	No. of days from seed placement until seedling harvest.
Absolute growth rate	AGR	g/day	Rate of mass increase relative to days to establishment.
<i>Resource allocation</i>			
Shoot mass fraction	SMF	0-1	Ratio of aboveground biomass to total plant biomass.
Root mass fraction	RMF	0-1	Ratio of belowground biomass to total plant biomass.
Leaf mass fraction	LMF	0-1	Ratio of leaf biomass to total plant biomass.
Hypocotyl mass fraction	HMF	0-1	Ratio of hypocotyl biomass to total plant biomass.
Specific hypocotyl length	SHL	mm/g	Ratio of hypocotyl length to hypocotyl biomass.
Total first true leaf area	TLA	cm ²	The area of the seedling’s first true leaf.

Results

Seedling Establishment

Experimental results supported the hypothesis that seedlings of large-seeded species have higher seedling establishment rates and higher AGRs compared to the seedlings of the small-seeded species under increasing CCSR levels. A significant interaction between CCSR levels and seed mass ($P < 0.01$) was observed in the analysis of the probability of seedling establishment (**Table 3-3**). The predicted probabilities of seedling establishment decreased as CCSR increased across seed mass levels, but the rate of decline was greater at lower seed mass levels (**Figure 3-2a**). Days to seedling establishment significantly increased as seed mass decreased and CCSR increased ($P < 0.0001$) (**Figure 3-2b; Table 3-3**). A significant interaction effect between CCSR levels and seed mass ($P < 0.05$) was detected in the analysis of AGRs during the seedling establishment phase (**Table 3-3**). The AGR increased as seed mass increased and decreased as CCSR increased (**Figure 3-2c**).

Analysis of individual species showed a decrease in seedling establishment rates of broad-leaved species across all CCSR levels, but this relationship varied among monocotyledon species. The predicted probability of seedling establishment was greater than 60% across all CCSR levels for large-seeded weed species (*I. purpurea*, *S. angulatus*; **Table 4**). Predicted probabilities of seedling establishment were less than 60% at 6,720 kg ha⁻¹ and less than 25% at 10,080 kg ha⁻¹ for small-seeded species (**Table 4**). Days to seedling establishment significantly increased as CCSR levels increased for *A. artemisiifolia* and monocotyledon species but was invariant for other species (**Table 3-5; Appendix A**). AGRs of all species, except for maize, decreased with increasing CCSR levels, but only *A. artemisiifolia* and *D. sanguinalis* AGRs had a significant relationship with CCSRs (**Table 3-5; Appendix A**).

Resource Allocation Patterns

Experimental results support the hypothesis that CCSR levels are positively correlated with resource allocation to the hypocotyl ($P < 0.05$) and specific hypocotyl length ($P < 0.0001$) of broad-leaved species (**Table 3-3**). Seed mass and the interaction between CCSR and seed mass did not have a significant effect on the HMF. In analysis by species, allocation to the HMF was positively correlated with CCSR levels in all broad-leaved species (**Appendix B**). A significant interaction between CCSR levels and seed mass ($P < 0.05$) was observed in analysis of specific hypocotyl length (**Table 3-3**). Increasing CCSR significantly increased specific hypocotyl length of all species (**Figure 3-3**).

Experimental results showed only partial support for the hypothesis that the effect of CCSRs would influence resource allocation patterns during the seedling establishment phase and that greater seed mass mediates resource allocation tradeoffs. A significant positive correlation between seed mass and resource allocation to the LMF was observed ($P < 0.0001$) but CCSR and the interaction between seed mass and CCSR was not significant (**Table 3-3**). Except for soyabean, all broad-leaved species showed a positive correlation between CCSR and resource allocation to the LMF, but this trend was only significant in *A. artemisiifolia* and *S. angulatus* (**Appendix B**). Seed mass had a significant effect ($P < 0.0001$) on TLA, but CCSR and the interaction between CCSR and seed mass did not have a significant effect (**Table 3-3**). A significant interaction between CCSR and seed mass was not observed in analysis of SMF and RMF (**Table 3-3**). However, as seed mass increased, biomass allocated to the SMF significantly

decreased ($P < 0.05$) and RMF significantly increased ($P < 0.05$). In analysis of species by CCSR interactions, increasing CCSR increased the SMF ($P < 0.05$) and decreased the RMF ($P < 0.05$) for broadleaved species, including *A. artemisiifolia*, *A. theophrasti*, *S. angulatus*, and soyabean (**Figure 3-4; Appendix B**). Increasing CCSR did not significantly affect the SMF and RMF of monocotyledon species (**Appendix B**).

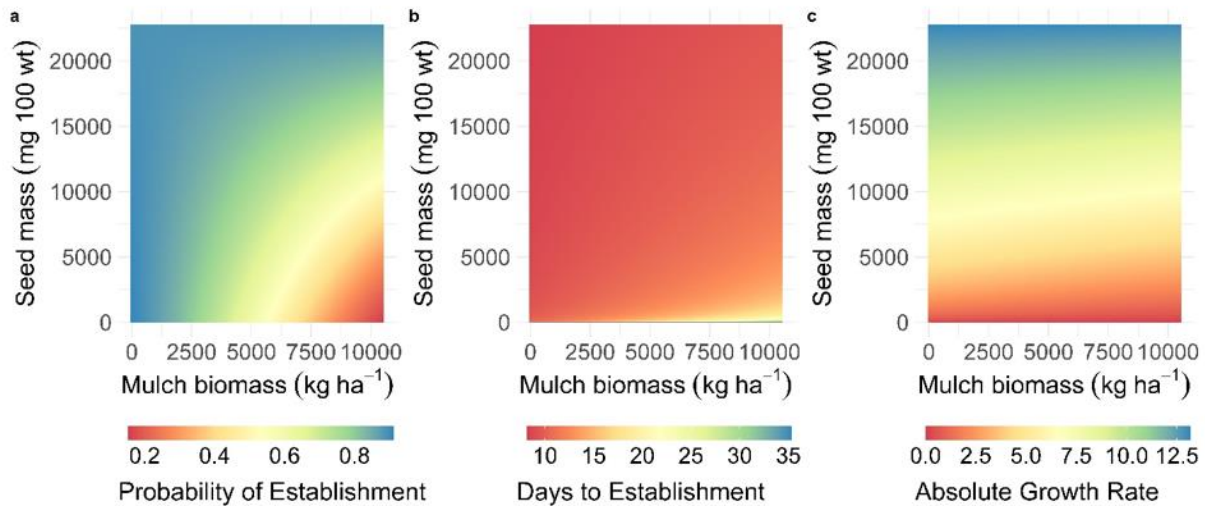


Figure 3-2. (a) Predicted probability of seedling establishment; (b) the number of days to establishment; and (c) absolute growth rates (AGRs) during the establishment phase as a function of seed mass (mg 100 wt) and cover crop surface residue (CCSR; kg ha⁻¹).

Table 3-3. Results of seedling establishment and resource allocation metrics modeled as a function of seed mass, cover crop surface residue, and their interaction.

Response variables	Treatment effects			R ² ††
	seed mass	CCSR [†]	seed mass*CCSR	
<i>Seedling establishment</i>				
Probability of establishment	<i>ns</i>	<0.0001	<0.01	0.29
Days to establishment	<0.01	<0.0001	<0.0001	0.36
Absolute Growth rate	<0.0001	<0.001	<0.05	0.81
<i>Resource allocation</i>				
Hypocotyl mass fraction	<i>ns</i>	<0.05	<i>ns</i>	0.24
Leaf mass fraction	<0.0001	<i>ns</i>	<i>ns</i>	0.27
Shoot mass fraction	<0.05	<i>ns</i>	<i>ns</i>	0.09
Root mass fraction	<0.05	<i>ns</i>	<i>ns</i>	0.09
Specific hypocotyl length	<0.0001	<0.0001	<0.05	0.85
Total first true leaf area	<0.0001	<i>ns</i>	<i>ns</i>	0.62

[†]CCSR = cover crop surface residue; ^{††}R² = marginal coefficient of determination for all linear regression models and McFadden's coefficient of determination for logistic regression model, probability of establishment.

Table 3-4. Predicted probability of seedling survival to establishment by dicotyledon and monocotyledon species at three cover crop surface residue (CCSR) levels (kg ha⁻¹).

Plant species [†]	Cover crop surface residue mass (kg ha ⁻¹)			
	0	3360	6720	10080
Dicotyledon spp.	----- Probability of seedling establishment (95% CI) -----			
<i>A. palmeri</i>	0.76 (0.40, 0.92)	0.31 (0.14, 0.56)	0.07 (0.01, 0.34)	0.01 (0.00, 0.22)
<i>A. artemisiifolia</i>	0.94 (0.69, 0.99)	0.79 (0.53, 0.93)	0.47 (0.26, 0.69)	0.17 (0.04, 0.49)
<i>A. theophrasti</i>	0.88 (0.59, 1.00)	0.71 (0.47, 0.87)	0.45 (0.25, 0.66)	0.21 (0.06, 0.52)
<i>I. purpurea</i>	0.98 (0.69, 1.00)	0.93 (0.69, 0.99)	0.83 (0.62, 0.94)	0.63 (0.31, 0.87)
<i>S. angulatus</i>	0.90 (0.60, 0.98)	0.84 (0.62, 0.94)	0.75 (0.55, 0.88)	0.64 (0.32, 0.86)
<i>G. max</i>	0.97 (0.60, 1.00)	0.95 (0.74, 0.99)	0.93 (0.75, 0.98)	0.90 (0.52, 0.99)
Monocotyledon spp.				
<i>D. sanguinalis</i>	0.99 (0.81, 1.00)	0.94 (0.62, 0.99)	0.50 (0.24, 0.77)	0.06 (0.01, 0.40)
<i>S. faberi</i>	0.79 (0.49, 0.95)	0.58 (0.37, 0.77)	0.34 (0.17, 0.57)	0.16 (0.04, 0.46)
<i>S. bicolor</i>	0.99 (0.83, 1.00)	0.96 (0.66, 1.00)	0.59 (0.30, 0.83)	0.08 (0.01, 0.44)
<i>Z. mays</i>	0.83 (0.52, 0.95)	0.78 (0.57, 0.90)	0.73 (0.53, 0.86)	0.67 (0.36, 0.88)

[†]Species listed from smallest to largest seed mass within dicotyledon and monocotyledon groups

Table 3-5. Fitted models of number of days to seedling establishment and absolute growth rate (AGR) during the establishment phase by plant species across CCSR treatments (kg ha⁻¹). Significance of slope coefficients are reported.

Plant species	days to establishment		AGR [†]	
Broad-leaved				
<i>A. artemisiifolia</i>	2.17 + 0.09x	**	-0.47 - 0.16x	*
<i>A. theophrasti</i>	2.31 + 0.04x	ns	0.21 - 0.02x	ns
<i>I. purpurea</i>	2.31 + 0.01x	ns	1.91 - 0.03x	ns
<i>S. angulatus</i>	1.99 + 0.007x	ns	2.25 - 0.009x	ns
<i>G. max</i>	2.05 + 0.03x	ns	2.76 - 0.02x	ns
Monocotyledon				
<i>D. sanguinalis</i>	2.48 + 0.18x	***	-1.11 - 0.24x	**
<i>S. faberi</i>	2.36 + 0.11x	**	-1.25 - 0.05x	ns
<i>S. bicolor</i>	2.19 + 0.13x	***	0.25 - 0.09x	ns
<i>Z. mays</i>	2.18 + 0.04x	**	1.88 - 0.02x	ns

[†] AGR = absolute growth rate; ^{††} Fitted slope coefficient and standard error (SE); Slopes significantly different from zero are denoted: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$

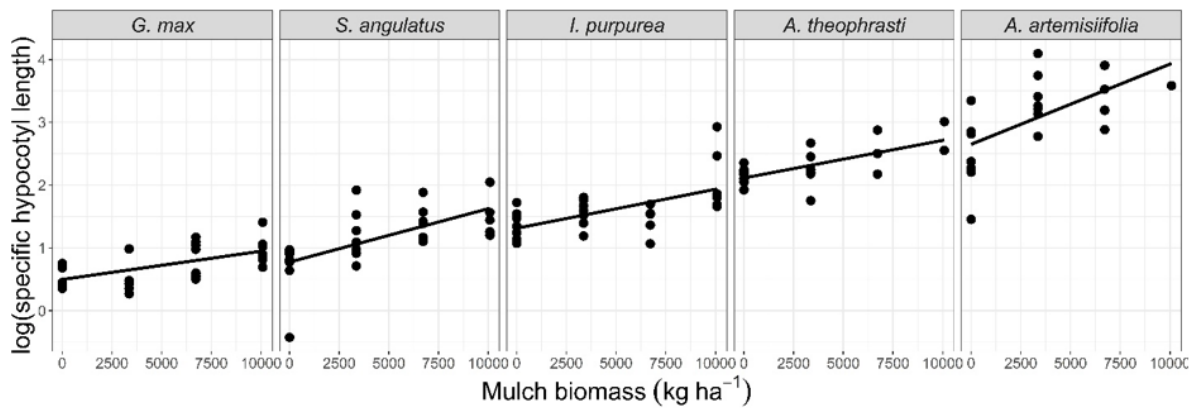


Figure 3-3. Relationship between specific hypocotyl length (natural log transformed) and mulch biomass (kg ha^{-1}) for broad-leaved species.

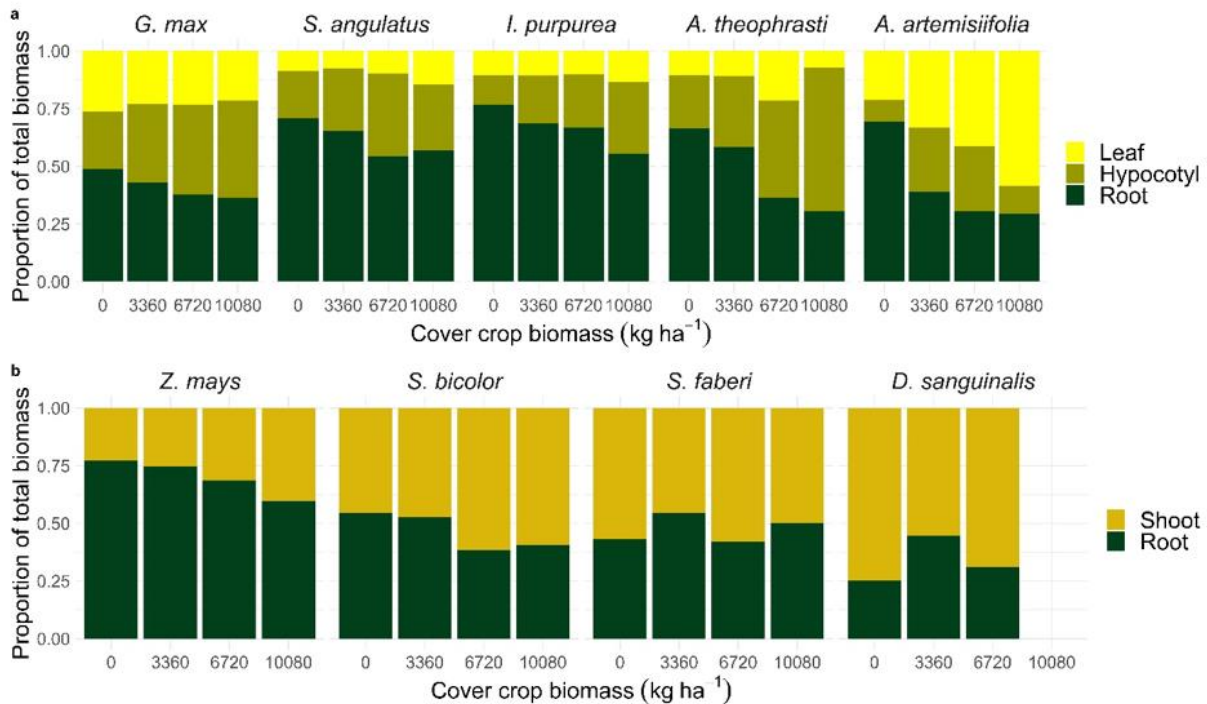


Figure 3-4. Proportion of total biomass allocation to (a) the leaf, hypocotyl, and root in broad-leaved species across cover crop biomass treatments; and (b) shoot and roots in monocotyledon species across surface residue biomass treatments.

Discussion

Our experimental results indicate that the effect of CCSRs on survival to establishment in the seedling establishment phase is a function of seed mass. Large-seeded weed species (*I.*

purpurea, *S. angulatus*) maintained high seedling establishment rates and AGRs across CCSR levels. Small-seeded weed species were comparatively more susceptible to increasing levels of CCSRs. Results of this study are consistent with previous studies conducted in non-arable habitats that have found similar fitness advantages for large-seeded species under shaded conditions created by plant litter (Leishman and Westoby, 1994; Moles and Westoby, 2004). Previous studies have shown that the level of weed suppression from phytotoxic properties of incorporated cover crop residues is inversely proportional to seed mass (Liebman and Sundberg, 2006; Kruidhof et al., 2011) and that differences in seed mass between crops, such as maize and soybean, and small-seeded weed species can create a fitness advantage for crops (Liebman and Gallandt, 2002;). To our knowledge, the present study is the first to quantify relationships between seed size and seedling establishment under CCSRs.

Our experimental results indicate that fatal germination in CCSRs may significantly contribute to weed suppression of small-seeded and economically important weed species in no-till production systems. At 6,000 kg ha⁻¹ of cereal rye surface residue, survival of emerging seedlings to establishment was 50% or less for common no-till weed species, including broad-leaves *A. palmeri*, *A. artemisiifolia*, and *A. theophrasti*, and grasses, *D. sanguinalis* and *S. faberi*. In the past, high levels of cover crop biomass production (6,000 kg ha⁻¹) were limited to organic no-till systems (Mirsky et al., 2012) but increasing interest in planting green practices, where cover crop termination is delayed to achieve multiple ecosystem services in no-till production systems (Reed et al., 2019), may hasten the adoption of CCSRs as a primary weed suppression tactic.

Given that the probability of establishment of large-seeded species, such as *S. angulatus* and *I. purpurea*, exceeded 60% across all CCSR levels, achieving meaningful suppression via CCSRs may not be feasible within the Mid-Atlantic U.S. region. It follows that adoption of high-residue cover cropping practices might select for a greater proportion of large-seeded dicot weeds over time. However, the implications of high fatal germination rates of small-seeded species within CCSRs on long-term seedbank dynamics and weed community assembly requires consideration of how CCSRs mediate additional population processes across seed mass gradients, including germination rates, germination timing, and fecundity (Leishman et al., 2000; Ganade & Westoby, 1999; Mohler, 1996).

Our experimental results indicate that CCSRs contribute to resource allocation patterns during the seedling establishment phase across seed mass gradients. Previous studies have shown that seedlings subjected to resource limitation during establishment achieve functional equilibrium of biomass allocation, in which relatively more biomass is allocated to structures that increase acquisition of the limiting factor (Poorter et al., 2012). As light becomes a limiting factor under increasing CCSR levels, broad-leaved crop and weed species increased resource allocation to shoot biomass, particularly to hypocotyl elongation, which came at a cost of reduced resource allocation to root biomass production. In monocotyledon species, allocation patterns were less consistent in response to CCSRs, likely due to differences in the relative position of apical meristems between broad-leaved and monocotyledon species. Previous studies have shown that a greater proportion of total biomass was allocated to the roots in grass species compared to broad-leaved species (Gross et al., 1992). Reduced root biomass production, due to reallocation of resources to shoot biomass under CCSRs, could result in nutrient and water deficits as seed reserves become depleted during the seedling establishment phase. Though we observed similar resource allocation patterns of broadleaved species in response to CCSRs across seed mass gradients, total biomass production allocated to roots, shoots and first true leaves were significantly greater in large-seeded species. However, the fitness advantage of large-seeded species during the establishment phase diminishes post-establishment due to higher RGRs of small-seeded species.

Our results indicate that seed mass was a strong predictor of resource allocation to first true leaf structures. We attribute this pattern to greater seed reserves and lower carbon deficits among large-seeded species, which allows for investment in true leaf development as it is the last structure to be fully developed prior to establishment. Hypocotyl elongation is a well-known response to reduced light conditions (Ballaré et al., 1991; Bruce et al., 2006; Ganade and Westoby, 1999), and our results show that allocating resources towards hypocotyl elongation contributes to seedling mortality of small-seeded species that germinate under CCSRs. We found that small-seeded species elongated their hypocotyl with a lower tissue density compared to large-seeded species across increasing CCSR levels, whereas large-seeded species constructed hypocotyls that were less affected by CCSR levels, likely due to greater seed reserves. Although increasing resource allocation to hypocotyl elongation resulted in photosynthetic autotropism and establishment of small-seeded species, it came at cost to hypocotyl tissue density, which likely

increases the susceptibility of seedlings to additional forms of stress (Ganade and Westoby, 1999).

Several studies have demonstrated that CCSRs can reduce selection pressures that drive the evolution of herbicide resistance by reducing weed population densities (Loux et al., 2017; Montgomery et al., 2018; Wiggins et al., 2015) and the size of individuals (Wallace et al., 2019; Bunchek et al., 2020) at the time of herbicide exposure. Beyond reduced selection pressure, the indirect effects of CCSRs on resource allocation during the seedling establishment phase, which we describe in this study, present opportunities for synergism with complementary weed control tactics. Previous studies have reported synergistic effects of CCSRs on herbicide efficacy, which the authors concluded was a result of a lower herbicide concentration, or effective dose, needed to control weed seedlings because of seedling resource exhaustion caused by CCSRs (Teasdale et al., 2005). Synergistic effects may be extended to other management interventions. For example, high-residue cultivation may result in greater efficacy in CCSR systems if weed species are comparatively more susceptible to partial-burial, severing of roots from shoots, or desiccation that result from mechanical weed control tactics. Consequently, the combined effects of CCSRs on seedling establishment rates and resource allocation and acquisition patterns can be a strong component of IWM strategies in no-till systems and will likely have differential effects on population trajectories for small- and large-seeded weed species.

Management Implications

Use of cover crop management tactics targeted to maximize cover crop biomass will impact weed communities and additional weed control strategies. Prolonged use of these tactics will likely select for large-seeded broad-leaved species in weed communities. Additional weed management tactics to target these species is necessary to maintain control. Given that weeds are typically more susceptible to additional stress once established in CCSR systems, these cover crop management tactics also present an opportunity for synergism with additional weed management tactics to increase control of established individuals.

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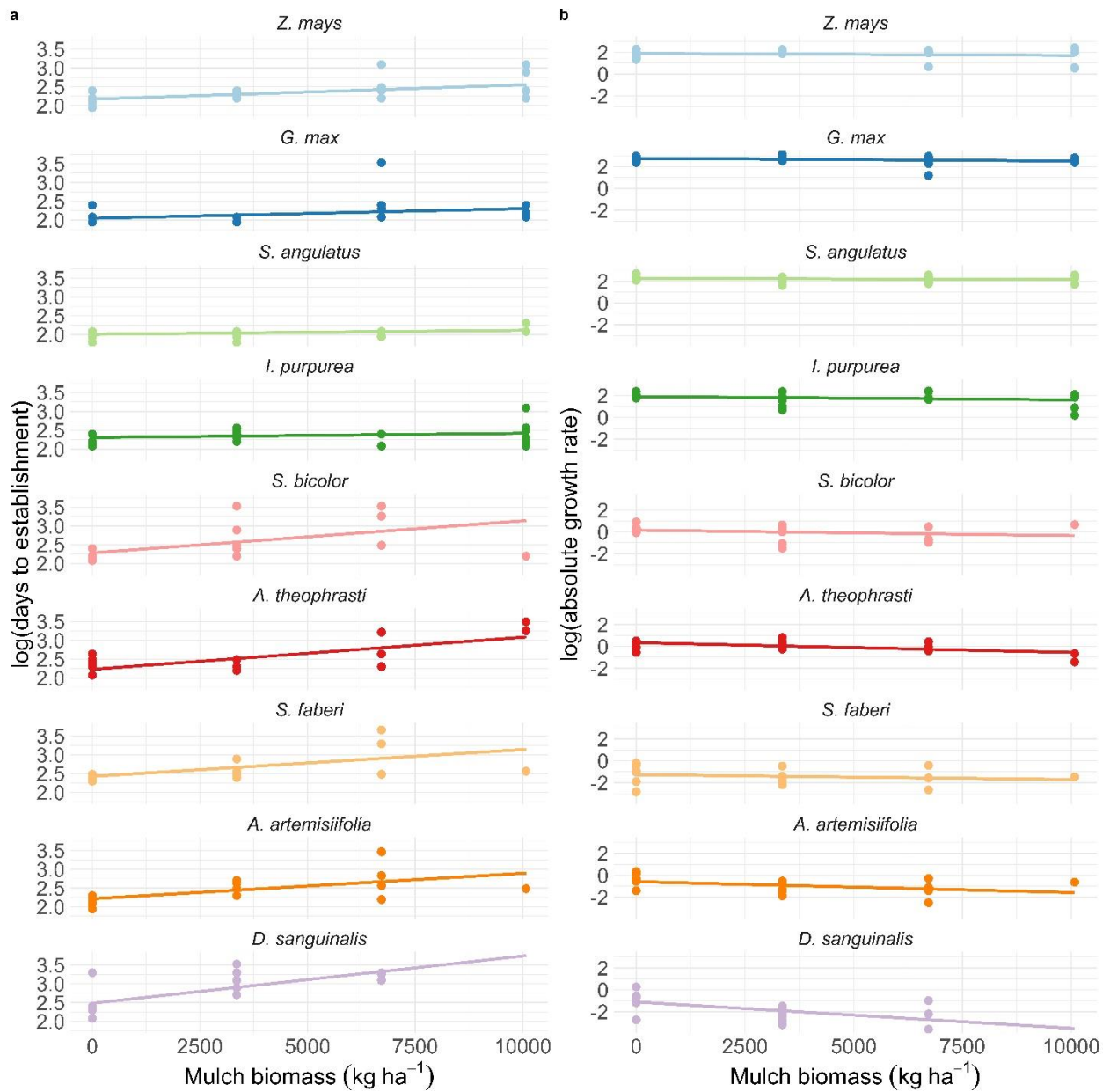
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Appendix A



(a) Log transformed response, days to establishment, regressed across CCSR treatments within each species. Data points represent log transformed response data. (b) Log transformed response, absolute growth rate, regressed across CCSR treatments within each species. Data points represent log transformed response data.

Appendix B

Fitted models of resource allocation patterns (HMF, LMF, RMF, SMF) by species. Significance of slope coefficients are reported.

Plant species	Resource allocation metrics							
	HMF [†]		LMF		RMF		SMF	
Broad-leaved								
<i>A. artemisiifolia</i>	0.29 + 0.03x	**	0.17 + 0.02x	*	0.54 – 0.05x	**	0.46 + 0.05x	**
<i>A. theophrasti</i>	0.37 + 0.02x	***	0.24 + 0.01x	*	0.44 – 0.03x	*	0.55 + 0.03x	*
<i>I. purpurea</i>	0.07 + 0.01x	***	0.05 + 0.001x	ns	0.40 – 0.006x	ns	0.59 + 0.006x	ns
<i>S. angulatus</i>	0.14 + 0.006x	ns	0.05 + 0.003x	*	0.46 – 0.01x	*	0.54 + 0.01x	*
<i>G. max</i>	0.16 + 0.01x	***	0.16 – 0.002x	ns	0.29 – 0.008x	**	0.71 + 0.008x	**
Monocotyledon								
<i>D. sanguinalis</i>	-	-	-	-	0.28 + 0.02x	ns	0.72 – 0.02x	ns
<i>S. faberi</i>	-	-	-	-	0.43 + 0.002x	ns	0.57 – 0.002x	ns
<i>S. bicolor</i>	-	-	-	-	0.52 – 0.02x	ns	0.48 + 0.02x	ns
<i>Z. mays</i>	-	-	-	-	0.73 – 0.006x	ns	0.27 + 0.006x	ns

[†]HMF = hypocotyl mass fraction, LMF = leaf mass fraction, RMF = root mass fraction, SMF = shoot mass fraction; Slopes significantly different from zero are denoted: * $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$