



**THE WEED COMMUNITY AFFECTS YIELD AND QUALITY OF SOYBEAN
(*GLYCINE MAX* (L.) MERR.)**

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Key Words:	Soybean, Seed quality and quantity, Non-metric dimensional scaling, Weed community



27 **Abstract:** The relationship between the weed community and soybean (*Glycine max* (L.)
28 Merr.) seed yield and quality was assessed in two soybean experiments in Illinois, USA.
29 One field was sown with different proportions of target weeds (*Ambrosia trifida* L.,
30 *Amaranthus rudis* J. Sauer, *Setaria faberi* F. Herrm), and the other was naturally infested
31 with these and other weeds. The composition of the weed communities in both fields
32 were compared to final yield and quality (% protein, oil, and water) of the crop using
33 NMDS ordination. Biomass and canopy cover, and seed quality (% protein, relative water
34 content, seed weight) of the crop, were related to the multivariate structure of the weed
35 community in both experiments. Lower quality soybeans were harvested from plots
36 dominated by the target weeds and a suite of subordinate volunteers. Analysis restricted
37 to the volunteer weed community was also significantly related to seed protein and seed
38 weight. Similar results from the two experiments lend generality to the findings and
39 indicate that soybean producers need to manage the composition of the weed community.

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41 **Keywords:** Soybean; Seed quality and quantity, Non-metric dimensional scaling; Weed
42 community.

43 **Running heading:** Weed community effects on soybean.

44 INTRODUCTION

45
46 Understanding the effects of weeds through competitive interactions on crop
47 plants has concerned agroecologists since the work of de Wit and colleagues in the
48 1960s.¹ However, most investigations have focused upon the interaction between the crop
49 and a single weed.² In reality, competitive interactions in communities are diffuse
50 involving multiple interactions among several species.³ The composition of the weed
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52 community is sensitive to the management conditions under which a crop is grown,⁴ and
53 can have a significant effect on the crop that transcends the effect of a single dominant
54 weed.⁵ The interactions among the multiple species of a weed community are likely non-
55 additive because the effects of all the species in a community is more than simply the
56 sum of individual pairwise interactions.⁶ There is, indeed, a high degree of
57 unpredictability of the outcome of multispecies competitive interactions⁷ that can lead to
58 uncertainty in making the correct weed management decisions. The implication of non-
59 additivity and diffuse competition in crop-weed systems is that crop yield loss can arise
60 from the complex interactions among the different species of the weed community rather
61 than simply the overriding effect of a single, dominant weed or the additive combination
62 of a mixture of weeds.

63 Soybean (*Glycine max* (L.) Merr.) is one of the most widely planted and
64 economically important annual crops in North America.⁸ Extensive soybean yield losses
65 can occur from weed competition⁹ and consequently, herbicides were applied to 98% of
66 the soybean production areas in the United States in 2005.¹⁰ Yield loss can occur
67 following multispecies interference from some weeds, e.g., pigweed (*Amaranthus* L.
68 spp.) and barnyard grass (*Echinochloa crus-galli* (L.) Beauv.).¹¹ Economic thresholds for
69 weed control in response suites of weeds have been developed,¹² but the decision-support
70 software is based upon simple additive models.¹³ In addition, most weed control efforts
71 in soybean are directed at understanding yield loss, and not necessarily seed quality, i.e.,
72 the seed oil and protein content. Seed quality is an increasingly important parameter in
73 determining the economic value and return from soybean¹⁴. There is a need to better
74 understand the multispecies nature of the weed community in soybean fields and the

75 extent to which they are related to both yield and seed quality. We report here on two
76 experiments conducted to assess the relationship between multispecies weed
77 communities and soybean yield and seed quality. We show significant yield and seed
78 quality losses related to a suite of weeds viewed as the whole community.

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MATERIALS AND METHODS

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Two parallel experiments were established in 2005, both in soybean fields. The
83 two experiments allowed us to assess the effect of comparable weed communities one
84 sown experimentally (the mesocosm experiment) and the other (the natural experiment)
85 arising entirely through volunteer establishment on crop yield and quality. In the
86 mesocosm experiment, three target weeds common waterhemp (*Amaranthus rudis* J.
87 Sauer), giant ragweed (*Ambrosia trifida* L.) and giant foxtail (*Setaria faberi* F. Herrm)
88 were sown experimentally to obtain plots with a range of weed densities. In the natural
89 experiment, the same target weeds were allowed to volunteer into a soybean field and
90 plots were located that would include the full range of weed densities planted in the
91 mesocosm experiment.

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The mesocosm experiment

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The experiment was established in a 0.3 ha agricultural field (37°70' N, 89°23'
96 W) at the Southern Illinois University, Agronomy Research Center, Carbondale, IL,
97 USA. The field site was previously used for agronomic crop production with intensive
98 weed management practices to reduce indigenous weed infestations. Furthermore, the
99 weed species investigated in this research were not common to the site. Soybean (*Glycine*
100 *max* cv. 'Asgrow 4403') was sown on May 18, 2005 using a commercial grain drill (John

101 Deere 750) with a row spacing of 17.5 cm at three densities (247,100, 423,425, and
102 617,750 seed ha⁻¹) as six randomly allocated strips in each of two 35 m wide x 18 m long
103 blocks.

104 Two rows of five 4.6 m x 3.7 m plots were established in each density of soybean
105 (n = 60 plots per block). Mixtures of the three target weeds were sown into each plot on
106 May 18, 2005. Seed were hand broadcast into the plots at one of three levels of total
107 weed density (0, 80,000 and 600,000 seed ha⁻¹). Seeds of *A. trifida* and *S. faberi* were
108 sown first after which the plots were lightly raked. *Amaranthus rudis* seed was broadcast
109 last and the plots where then the soil was lightly tamped. The weed seed for *A. trifida*
110 and *A. rudis* was collected from mature plants in autumn 2003 from naturally infested
111 fields at the Belleville Research Center. Seed for *S. faberi* was collected from mature
112 plants in autumn 2003 from naturally infested fields at the Agronomy Research Center.

113 The relative abundances of weeds in the weed mixture were manipulated using a
114 Simplex design.^{15, 16} Weed mixtures were either monocultures (one weed only sown),
115 each weed represented equally, or intermediate points, with one weed being subordinate
116 (10% proportionally) and the other two being equally represented (45%). Densities of
117 weeds sown for each weed species were based on equivalents between weed species
118 supplied by Weedsoft ®.¹³ The weeds were oversown by 100% to account for low
119 germination rates or seedling establishment.

120 The plots were weeded to remove non-target weeds once over the course of the
121 experiment, on June 27-28 between sample 1 and sample 2.

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Natural experiment

125 This experiment was established in a 0.4 ha agricultural field (38 ° 51' N, 89° 84'
126 W) at Belleville Research Center, Belleville, Illinois, USA, 104 km NNW of the
127 mesocosm experiment. Soybean (*Glycine max* cv. 'Asgrow 4403') was sown on May 17,
128 2005 using a commercial grain drill (Great Plains) with a row spacing of 17.5 cm at three
129 densities (247,100, 423,425, and 617,750 seed ha⁻¹) as 15 randomly allocated strips in
130 each of two 46 m wide x 46 m adjacent blocks. Each soybean row was divided into ten 3
131 m wide x 4.5 m long plots (n = 150 per block). Weeds were allowed to naturally
132 volunteer in these plots and we identified 69 plots on June 17-18 that contained the same
133 relative proportions of the target weeds that were sown in the mesocosm experiment (i.e.,
134 monocultures of each weed, and mixtures of the target weeds). Non-target weeds were
135 hand-removed from the plots on June 17-18 prior to the first survey.

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138 **Data collection**

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140 Data were collected during four surveys of the plots in both experiments on June
141 8, August 1 – 3, September 17, and October 7 – 30 from the mesocosm, and June 17, July
142 26-27, September 10-11, and October 23-25 from the natural experiment. The first three
143 survey dates corresponded to soybean growth stages of V2-V3, R2-R3, and R6, and the
144 final date was a final harvest when the soybean pods were mature.

145 Canopy cover of all vascular plant species in each plot was estimated using a 7-
146 point modified Daubenmire scale¹⁷ for the first three surveys. The mid-point of each
147 cover class was used in subsequent analyses. Soybean and target weed density estimates
148 were determined by counting stems in two 0.5 m² quadrats that were randomly located
149 for the first survey within each plot. The corners of the quadrats were marked with wire

150 flags to allow exact relocation for subsequent surveys. Aboveground biomass of
151 individual soybean plants was estimated by harvesting an average-sized individual from
152 outside of the quadrat survey areas on each survey date. The harvested individual was
153 oven dried to constant weight at 60 ° C and weighed. Final standing crop of soybean and
154 each target weed was determined by harvesting pooled weights (oven dry basis) of all
155 plants from within the two 0.5 m² quadrats. Total yield was obtained by stripping and
156 weighing the soybeans from the soybean plants obtained from each plot. The biomass of
157 a random subsample of soybeans from each plot was used to calculate 100-seed weight.
158 Relative Water Content (RWC) was obtained by sampling one leaflet from the upper 1/3
159 of a soybean plant in each plot and placing it in a tarred vial filled with deionized water.
160 Fresh weight (FW) of the leaflet was obtained by subtracting the weight of the tarred vial
161 from the vial with leaf. The vial with leaflet was left overnight at 4°C in the dark, then
162 weighed to obtain turgid weight (TW). The leaflet was then dried at 60°C, and weighed
163 to obtain dry weight (DW). RWC was calculated by the following equation:

$$164 \quad \text{RWC} = 100 * (\text{FW} - \text{DW}) / (\text{TW} - \text{DW})$$

165 Percent water, oil, and protein was determined from whole seed samples using a Zeltex
166 ZX-50 portable grain analyzer (Zeltex, Inc., Hagerstown, Maryland).

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169 **Data analyses**

170 A multivariate approach was used to quantify the relationship between the weed
171 community and soybean seed yield and quality.¹⁸ Canopy cover data from the two
172 experiments were analyzed using non-metric dimensional scaling NMDS:¹⁹ a non-
173 parametric ordination method that has been shown to be a robust technique for

174 multivariate analysis²⁰, using the program DECODA.²¹ Separate ordinations were
175 undertaken for each of the two experiments. The canopy cover data were standardized to
176 adjust species to unit maxima prior to analysis based on the Bray-Curtis dissimilarity
177 coefficient. Canopy cover of the crop *Glycine max* was not included in the data matrix
178 for ordination analysis. Twenty random starting configurations were initiated running up
179 to 200 iterations to obtain 1 – 4 dimensional solutions. The minimum number of
180 dimensions necessary to obtain a useful interpretation of the data was retained after
181 inspection of stress plots, minimum stress with R-values, and plots of significant vectors
182 and species centroids (see below).

183 The relationship of the abundance of species to the retained ordination solution
184 was assessed by calculating species scores for each species in the NMDS space. The
185 species scores were calculated as the weighted average of the abundance scores of the
186 samples in which the species occurred in for each dimension. These weighted averages
187 were used to plot species as points in the NMDS ordination and are referred to as species
188 centroids because they show the center of the species' distribution with respect to the
189 ordination axes.

190 The relationship between the ordination solution and independent variables,
191 including time, experimental block, initial proportions and sowing densities of the
192 planted weeds (mesocosm experiment only), density and evenness calculated as
193 Simpson's Evenness²², of the target weeds, and crop yield and quality variables, was
194 investigated by fitting vectors of maximum correlation. Vector significance was assessed
195 following permutation tests to generate correlation values. Vectors significantly
196 correlated with the ordination were retained for plotting in ordination space relative to the

197 ordination centroid. The soybean seed yield and quality variables were measured at final
198 harvest, later than the last canopy cover survey. The relationship between these variables
199 and the ordination was assessed in two ways; i) the values for each variable were used to
200 calculate vectors in a single analysis by assessing the values versus the plots for each
201 survey separately and ii) by repeating the values versus the plots for each survey in one
202 analysis. Significant vectors obtained from the first procedure were retained for
203 interpretation except when a single significant vector for the single analysis adequately
204 represented the three vectors calculated independently. The abundance of species in plots
205 arranged along vectors of particular interest (e.g., those for seed protein) were examined
206 by constructing two-way ordered tables.

207 The relationship between *a priori* defined groups (i.e. time and block) and the
208 weed community in each experiment was tested using Analysis of Similarity ANOSIM:
209 ²³ in DECODA. ANOSIM compares within- versus among-group similarity based upon
210 the Bray-Curtis dissimilarity coefficient by 1000 random permutations of group
211 membership to calculate an R-value constrained to a range of -1 to 1 where a value of 1
212 indicates that all plots within a group are more similar to each other than to members of
213 another group. The significance of the R-value is determined as the proportion of
214 permuted R-values greater than or equal to the original.

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RESULTS

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228 **Crop yield and quality**

229 In the mesocosm plots, soybean yield was $538.0 \pm 54.0 \text{ kg ha}^{-1}$ ($n = 114$; $543.0 \pm$
230 54.0 kg ha^{-1} in 11 plots planted as soybean monocultures), mean one-hundred seed
231 weight was $10.0 \pm 0.3 \text{ g}$ ($n = 103$), water content $5.1 \pm 0.1 \%$, protein content 40.2 ± 0.2
232 $\%$ and oil content $21.5 \pm 0.1 \%$ ($n = 93$ for water, protein and oil content).

233 In the natural experiment, soybean yield was $694.0 \pm 46.0 \text{ kg ha}^{-1}$ ($n = 68$), mean
234 one-hundred seed weight was $12.8 \pm 0.1 \text{ g}$ ($n = 65$), water content $5.2 \pm 0.1 \%$, protein
235 content $39.1 \pm 0.1 \%$ and oil content $22.5 \pm 0.1 \%$ ($n = 68$ for water, protein and oil
236 content).

237

238 **Mesocosm experiment**

239 The planted weeds dominated the weed flora in the mesocosm plots with
240 *Ambrosia trifida* having the highest abundance and *Setaria faberi* being most frequent
241 (Table 1). The mean number of species per plot, including soybean, ranged from 4 to 7.2
242 over the three surveys, with 24 volunteer weeds colonizing the plots. Some of the
243 volunteer weeds were common (e.g., *Mollugo verticillata* L. 100% at survey 1, *Ipomoea*
244 *hederacea* (L.) Jacq. 55% at surveys 1 and 2) with four achieving 37.5% canopy cover in
245 at least one plot (i.e., *Cyperus esculentus* L., *Cardamine parviflora* L., *Digitaria*
246 *sanguinalis* (L.) Scop., *Sorghum bicolor* (L.) Moench.).

247 There was a strong relationship between the weed community and sample date,
248 with time being a significant discriminating variable among groups of plots especially

249 between survey 1 and survey 2 (ANOSIM: $R = 0.30$, $p < 0.0001$, survey 1 vs survey 2, R
250 $= 0.44$, survey 1 vs 3 $R = 0.46$, 2 vs 3 $R = 0.06$, all $p < 0.0001$). There was a weak, albeit
251 significant, difference between the weed community among the two experimental blocks
252 (ANOSIM, $R = 0.05$, $p < 0.0001$).

253

254 (Figure 1 location)

255

256 A 3-dimensional NMDS solution was retained for interpretation (stress = 0.17)
257 and the structure of the ordination strongly reflected survey date (Fig 1). The centroids of
258 the distributions of the three planted weeds were separated in the ordination. A group of
259 early season volunteer weeds characterized plots at survey 1, including *Sida spinosa* L.,
260 *Mollugo verticillata*, *Chamaesyce humistrata* (L.) Small, *Lamium amplexicaule* (L.)
261 Small, *Poa annua* L., *Solanum carolinense*, *Ranunculus abortivus* L., and *Oxalis stricta*
262 L. (Table 1, Fig 2). Later in the season following emergence after the plots were weeded,
263 the plots were characterized by some of the same species along with a new suite of
264 volunteers including *Sorghum bicolor*, *Paspalum leave* Michx., *Conyza canadensis* (L.)
265 Cronq., and *Xanthium strumarium* L.. Species such as *Cardamine parviflora*, *Digitaria*
266 *sanguinalis*, and *Ipomoea hederacea* were frequent throughout the season.

267

268 (Figure 2 location)

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270 Significant vectors related to the 3-dimensional solution indicated that the number
271 of species per plot decreased through time following weeding between survey 1 and 2,

272 and as crop canopy cover and biomass increased through the season (Table 2, Fig 3). The
273 original sown proportions of target weeds and evenness of their canopy cover were
274 related to the ordination, reflecting the later dominance of the weed flora by the target
275 weeds. Evenness of the target weeds also formed an obtuse angle with total yield, i.e.
276 increase in evenness is somewhat associated with reduced total yield. Total seed yield of
277 the crop, seed water content, one-hundred seed weight, and protein content were related
278 to the composition of the weed community. The vectors for these crop yield and quality
279 components were aligned away from the plots where the weed flora included high
280 abundance of *A. trifida*, and, to a lesser extent, the other planted weeds. Some weeds such
281 as the planted *S. faberi* were most abundant in the plots where *A. trifida* was at a low
282 abundance aligned with the seed quality (protein), seed water content and one-hundred
283 seed weight. Specifically, the vector for seed protein related to the weed community at
284 survey 1 showed that plots associated with the lowest seed protein were those with the
285 highest canopy cover of the planted *A. trifida* and volunteer *Ipomea hederacea* and
286 *Chamaesyce humistrata*. By contrast, plots associated with the highest seed protein had
287 the highest abundance of the planted *S. faberi*, the volunteer *Mollugo verticillata*,
288 *Digitaria sanguinalis* at survey 1 (App. 1), and overall the highest evenness of the target
289 weeds.

290

291 (Figure 3 location)

292

293 An NMDS ordination restricted to the volunteer weeds (3-dimensional NMDS
294 solution, stress = 0.15), i.e., without the planted target weeds, also showed a significant

295 relationship between the multivariate structure of the weed communities and seed quality,
296 including protein content at survey 2 ($r = 0.36$, $p = 0.012$, $n = 88$) and one-hundred seed
297 weight at survey 1 ($r = 0.39$, $p = 0.002$, $n = 103$). Similarly, an NMDS ordination restricted
298 to only the planted weeds (3-dimensional NMDS solution, stress = 0.09) was related
299 significantly to one-hundred seed weight ($r = 0.37$, $p < 0.0001$, $n = 296$) and total yield (r
300 = 0.42, $p < 0.0001$, $n = 329$), but not seed oil or protein content.

301

302 **Natural experiment**

303 The target weeds dominated the weed communities that volunteered into the
304 natural experiment with *A. trifida* having the highest canopy cover, exceeding that of the
305 crop, and occurring in 100% of the plots (Table 3). The mean number of species per plot,
306 including soybean, ranged from 5.1 to 6.9 over the three time periods, with 20 unplanted
307 weeds colonizing the plots. In addition to the three target weeds, *Ipomoea hederacea*,
308 *Abutilon theophrastii* Medic, and *Panicum dichotomiflorum* Michx. occurred in > 50% of
309 the plots during at least one survey, with *Amaranthus retroflexus* L. reaching 15% canopy
310 cover in at least one plot.

311 There was a strong relationship between the weed community and sample date,
312 with time being a significant discriminating variable among groups of plots especially
313 between survey 1 and survey 3 (ANOSIM: $R = 0.20$, $p < 0.0001$, survey 1 vs survey 2, R
314 = 0.17, survey 1 vs 3 $R = 0.32$, 2 vs 3 $R = 0.15$, all $p < 0.0001$). There was only a weak
315 difference between the weed communities among the two experimental blocks
316 (ANOSIM, $R = 0.07$, $p < 0.0001$).

317

318 (Figure 4 location)

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320 A 2-dimensional NMDS solution was retained for interpretation (stress = 0.27)
321 and the structure of the ordination strongly reflected survey date (Fig 4, Table 4). The
322 centroids of the distributions of the three target weeds were centrally located in the
323 ordination (Fig 5). A group of early season volunteer weeds characterized plots at survey
324 1, including *Amaranthus retroflexus*, *Cyperus esculentus*, *Ampelamus albidus* (Nutt.)
325 Britt., and *Sida spinosa* with a different suite of species characterizing the plots later in
326 the season including *Persicaria pensylvanicum*, *Xanthium strumarium*, *Hordeum pusillum*
327 Nutt., and *Panicum dichotomiflorum*, and (Table 3, Fig 5). *Ipomoea hederacea* and
328 *Ambrosia artemisiifolia* L. were frequent throughout the season.

329

330 (Figure 5 & Figure 6 location)

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332 Significant vectors related to the 3-dimensional solution indicated that the number
333 of species per plot decreased through the season as crop biomass increased (Table 4, Fig
334 6). Soybean biomass and canopy cover, relative water content, and seed protein content
335 of the crop were related to the composition of the weed community. Although not
336 planted, the density and biomass of the two of the target weeds (*Amaranthus rudis*,
337 *Setaria faberi*) were significantly related to the 2-dimensional solution. The vectors for
338 crop seed quality (relative water content and protein content) were aligned towards plots
339 containing the highest density of *Setaria faberi*, and high frequency and abundance of
340 *Solanum carolinense* and *Digitaria sanguinalis*, and away from plots with high amounts

341 of *Amaranthus rudis* and weeds of minor importance including *Eragrostis trichodes*
342 (Nutt.) Wood (Fig 6). The vector for seed protein and the weed community at survey 3
343 indicated that the highest levels of seed protein were associated with plots in which the
344 weed community was characterized by the *Ambrosia artemisiifolia* and *Ipomoea*
345 *hederacea* and low amounts of the target weed *Amaranthus rudis* (App. 2). Soybean yield
346 components were unrelated to the 2-dimensional weed community ordination. Seed oil
347 content and 100 seed weight were related to a 3-dimensional solution (not presented), but
348 little extra interpretative value with respect to the importance of the weed community was
349 attributed to this solution.

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DISCUSSION

355 Together the two experiments confirm that the abundance (density, biomass,
356 cover), and seed yield and quality of soybean were related to the composition of the weed
357 community. This consistent result was obtained both in plots planted with weeds (the
358 mesocosm experiment) and in plots allowed to become naturally infested with weeds (the
359 natural experiment). The mesocosm experiment was planted at a site where the three
360 target weeds (*Amaranthus rudis*, *Ambrosia trifida*, and *Setaria faberi*) were not expected
361 to occur, allowing their planting densities to be controlled. The natural experiment was
362 conducted at a site that had a prior history of high abundance of these three weeds so that
363 they would naturally infest the crop. The target weeds dominated the plots as expected,
364 and soybean seed yield and quality was significantly related to their abundance,
365 especially *A. trifida* (the quantitative nature of this relationship will be reported

366 elsewhere). Indeed, *A. trifida* is one of the most aggressive weeds in soybean fields
367 reducing yield at less than two plants per 9 m of soybean row.²⁴

368 Variation in soybean seed quality affects its economic value as a crop.¹⁴ Both seed
369 protein and oil content can vary among cultivars and in response to environmental
370 conditions.²⁵⁻²⁷ Seed protein content varies more than seed oil content, although the two
371 are inversely related to each other.²⁸ Our experiments showed a relationship between seed
372 protein content and the weed community, but no relationship to seed oil content.
373 Numerous studies with a variety of crops and weed species have clearly established that
374 increasing competition negatively impacts yields.²⁹ However, the impact of weed
375 competition upon seed quality (i.e. protein and oil content) has not been extensively
376 studied. Previous research with soybean has demonstrated that the protein content of soy
377 seeds was unaffected by altered densities of the weedy species *Trianthema*
378 *portulacastrum* L.³⁰ However, in the legume *Lathyrus sativus* L., protein content did
379 increase within plots containing a mixture of weedy species (i.e. *Chenopodium album* L.,
380 *Avena fatua* L. and *Setaria viridis* (L.) P. Beauv.), and the increase was attributed to
381 decreased seed size (i.e. dry matter content).³¹ In the experiments described here, the
382 protein content of soybean seeds was altered in both mixed species competition and
383 single species competition. Protein content increased under high weed density conditions
384 with both *Amaranthus rudis* and *Setaria faberi*, while decreasing under high weed
385 density conditions with *Ambrosia trifida* (Figures 2,3,5 & 6).

386 Results of the mesocosm experiment suggested that soybean yield was most
387 closely related to the abundance of the target weeds (planted density and evenness: Fig
388 3), whereas seed quality, specifically protein content, was related to the composition of

389 the volunteer weed community. The target weeds were more abundant than the volunteer
390 weeds and so might be expected to reduce soybean yield. That the community of less
391 abundant volunteers was also related to soybean seed quality suggests a more subtle
392 relationship with the soybean plants than that exerted by the target weeds in reducing
393 yield. There appears to be a diversity/synergy interaction among members of the weed
394 community affecting soybean.³² Potential resources known to affect seed protein content
395 that the volunteer weed community may have been competing for with soybean for
396 include soil moisture and nutrients.^{33,34} The low canopy cover of the volunteer weeds
397 suggests that aboveground competition for light was unlikely to have affected seed
398 protein. Within-field variation in seed protein content of a similar magnitude as we
399 observed (i.e., < 2% or 2 g kg⁻¹) has been previously attributed to spatial variation in soil
400 nitrogen;³³ which itself may vary in response to competition with the weed community
401 and may have affected the weed community particularly in the natural experiment.
402 Significant genotype by environment interactions can affect soybean seed protein content
403 to a similar extent,^{35,36} although the environmental component has not previously been
404 attributed to the effects of weed competition.

405 Soybean yield and seed quality were related to the weed community in different
406 ways in the natural experiment. The occurrence of these differences suggests that the
407 soybean simultaneously had to compete with different groups of weeds, more than likely
408 for a different suite of resources. In this case, aboveground competition for light with
409 large weeds such as *Ambrosia trifida* was reducing soybean yield, while belowground
410 competition for soil resources with minor weeds including *Solanum carolinense* and
411 *Digitaria sanguinalis* was reducing seed quality. Both *S. carolinense* and *D. sanguinalis*

412 are known infest soybean fields and their growth forms are more conducive for
413 belowground than aboveground competition with soybean.^{37,38} An effect of these two
414 species on soybean seed quality is previously unreported.

415 There was also a temporal dynamic to the weed-crop relationship as the weed
416 communities changed through the season with spring emerging plants dominating early
417 on being replaced with later season weeds towards the end of the season. The relationship
418 between the early season weed community (i.e., at the first survey) and final soybean
419 seed water and protein content in the mesocosm experiment suggests that early season
420 interactions between non-reproductive soybean (V2-V3 stages) and weeds are
421 sufficiently important to manifest their effects late in the season. Previous studies has
422 shown that early season weed infestation can significantly reduce soybean yield³⁸, but
423 less is known about how these early season factors affect seed quality. By contrast, the
424 natural experiment suggested that the effects of the weed community on soybean
425 biomass, yield and seed quality (protein) were the results of only late season interactions
426 (i.e., when the soybeans were at the R2-R3 stage). Overall, the implication is that the
427 magnitude and importance of different types of competitive interactions vary through the
428 season.³⁹ Previous studies have indicated that there are critical times important for weed
429 removal in soybean to minimize yield losses^{40,41} supporting this observation.

430

431 **Conclusion**

432

433 The multivariate analytical approach that we use here is circumstantial and
434 retrospective,⁴² however, it allows inferences to be made regarding the mechanistic basis

435 for the patterns observed because of the experimental nature of the mesocosm
436 experiment. We have interpreted the relationships between the crop and the weed
437 communities in terms of competitive interactions. Alternatively, the weed communities
438 may be reflective of environmental spatial heterogeneity in the crop fields to which both
439 the crop and the weeds were responding. In other words, the weed community may be an
440 indicator of conditions, such as areas of droughty or degraded soil, that is directly
441 affecting both the weed community and crop seed yield and quality.^{5, 43} Nevertheless,
442 decision-support software can accurately predict yield loss in soybean from weeds,⁴⁴ but
443 does not provide an integrated and multivariate or non-additive account of mixed-weed
444 communities. Our approach has shown that the diffuse nature of the weed community
445 may be of importance for understanding both yield and seed quality loss in soybean. The
446 weed communities in crops are likely to increase in diversity and complexity as reduced
447 tillage practices are increasingly adopted⁴⁵ making an understanding of the relationship
448 between the weed community and the crop particularly important.⁴⁶

449

450

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Table 1. Species abundance from the mesocosm. *Glycine max*, *Ambrosia trifida*, *Amaranthus rudis*, and *Setaria faberi* were planted, other species (below dotted line) were volunteers (ordered by frequency at survey 1, and survey 2, respectively).

Species/survey	Mean			Max cover (%)	Frequency (% of 120 plots)		
	canopy cover (%)				1	2	3
	1	2	3				
<i>Glycine max</i> (L.) Merr.	2.8	15.1	5.1	85.0	100	98	97
<i>Ambrosia trifida</i> L.	3.5	27.4	20.1	97.5	58	69	64
<i>Amaranthus rudis</i> J. Sauer	0.3	0.7	3.2	37.5	44	34	62
<i>Setaria faberi</i> F. Herrm	1.5	9.8	10.1	97.5	85	76	70
<i>Mollugo verticillata</i> L.	0.7	0	0	3.0	100	0	0
<i>Chamaesyce humistrata</i> (L.) Small	0.4	0.004	0	0.5	78	1	0
<i>Ipomoea hederacea</i> (L.) Jacq.	0.6	0.8	0.1	15.0	55	55	12
<i>Digitaria sanguinalis</i> (L.) Scop.	0.9	0	2.8	37.5	54	0	23
<i>Sida spinosa</i> L.	0.2	0	0	0.5	36	0	0
<i>Oxalis stricta</i> L.	0.2	0.004	0.1	3.0	31	1	10
<i>Cyperus esculentus</i> L.	0.2	0.004	0.9	37.5	31	1	3
<i>Chenopodium album</i> L.	0.6	0.7	0	15.0	24	19	0
<i>Cardamine parviflora</i> L.	0.04	0.01	1.4	37.5	8	3	13
<i>Amaranthus retroflexus</i> L.	0.02	0.3	0.2	15.0	3	17	6

<i>Ambrosia artemisiifolia</i> L.	0.05	0.008	0	3.0	3	2	0
<i>Poa annua</i> L.	0.008	0.2	0	15.0	2	3	0
<i>Cerastium vulgatum</i> L.	0.008	0.004	0.025	3.0	2	1	1
<i>Xanthium strumarium</i> L.	0.004	0	0.3	15.0	1	0	12
<i>Lamium amplexicaule</i> L.	0.004	0	0	0.5	1	0	0
<i>Ranunculus abortivus</i> L.	0.004	0	0	0.5	1	0	0
<i>Solanum carolinense</i> L.	0.004	0	0	0.5	1	0	0
<i>Sorghum bicolor</i> (L.) Moench.	0	2.1	0.3	37.5	0	46	16
<i>Galium aparine</i> L.	0	0.3	0	15.0	0	11	0
<i>Physalis subglabrata</i> Mack. & Bush.	0	0.07	0	3.0	0	9	0
<i>Festuca arundinacea</i> Schreb.	0	0.06	0	3.0	0	8	0
<i>Paspalum leave</i> Michx.	0	0.02	0.2	15.0	0	3	8
<i>Conyza canadensis</i> (L.) Cronq.	0	0	0.01	3.0	0	0	5
<i>Persicaria pensylvanicum</i> (L.) Small	0	0	0.004	0.5	0	0	1
Average No. spp per plot*	7.2	4.6	4.0				

* including *G. max.*

Table 2. Correlations (R) and probability (P) of significant environmental vectors with 3-dimensional NMDS ordination of mesocosm cover data.

Variable	n	R	P
Time	360	0.80	< 0.0001
Block	360	0.24	< 0.0001
Sown Proportion <i>Ambrosia trifida</i> ¹ .	360	0.60	< 0.0001
Sown Proportion <i>Amaranthus rudis</i> ¹ .	360	0.37	< 0.0001
Sown Proportion <i>Setaria faberi</i> ¹ .	360	0.63	< 0.0001
Planting density target weeds	360	0.37	< 0.0001
Simpson's Evenness target weeds	347	0.53	< 0.0001
Soybean density	240	0.48	< 0.0001
Soybean biomass	359	0.51	< 0.0001
Soybean cover	360	0.35	< 0.0001
Soybean final density (at harvest) ³ .	360	0.25	< 0.0001
Soybean standing crop final biomass ⁴ .	342	0.30	< 0.0001
Number of species	360	0.72	< 0.0001
% seed protein ⁵ .	279	0.21	0.008
% seed water survey 1 ⁴ .	93	0.30	0.004
Soybean total yield ⁴ .	342	0.26	< 0.0001
100-seed-weight	309	0.31	< 0.0001

1. Vectors for planting densities of the three target weeds were also significant and aligned in the same direction as those for sown proportions.
2. Vector for protein at survey 1, $R = 0.27$, $P = 0.09$, $n = 93$ was aligned close to this composite vector.
3. Vectors for soybean final density were also significant for surveys 1 – 3 and were closely aligned to that of the composite vector shown.
4. Vectors for separate surveys were also significant with the composite vectors aligned close to those from survey 3 for Soybean total yield and survey 2 for soybean standing crop final biomass and 100-seed-weight, respectively.
5. A significant vector was obtained only for the relationship between the weed communities from survey 1 and % seed water.

Table 3

Species abundance from plots in the natural experiment. The crop *Glycine max* was planted, *Ambrosia trifida*, *Amaranthus rudis*, and *Setaria faberi* were target volunteers, other species (below dotted line) were volunteers (ordered by frequency at time 1, and time 2, respectively).

Species/survey	Canopy cover (%)			Max	Frequency (% of 69 plots)		
	1	2	3	cover (%)	1	2	3
					1	2	3
<i>Glycine max</i> (L.) Merr.	4.1	9.6	7.1	37.5	100	100	100
<i>Ambrosia trifida</i> L.	13.8	29.8	23.4	62.5	100	100	100
<i>Amaranthus rudis</i> J. Sauer	2.3	2.5	1.9	15.0	87	99	87
<i>Setaria faberi</i> F. Herrm	1.7	2.5	2.4	37.5	95	83	70
<i>Ipomoea hederacea</i> (L.) Jacq.*	1.3	1.0	0.9	3.0	84	88	57
<i>Abutilon theophrastii</i> Medic	0.7	0.5	0	3.0	53	58	0
<i>Ampelamus albidus</i> (Nutt.) Britt.	0.5	0.1	0	3.0	48	25	0
<i>Amaranthus retriflexus</i> L.	1.3	0	0	15.0	40	4	0
<i>Cyperus esculentus</i> L.	0.2	0.03	0	0.5	29	6	0
<i>Ambrosia artemisiifolia</i> L.	0.2	0.4	0.3	3.0	24	33	22
<i>Persicaria pensylvanicum</i> (L.) Small	0.2	0.01	0.1	3.0	8	3	10
<i>Sida spinosa</i> L.	0.03	0	0	0.5	7	0	0
<i>Digitaria sanguinalis</i> (L.) Scop.	0.03	0	0	0.5	7	0	0

<i>Chenopodium album</i> L.	0.02	0.01	0	0.5	5	3	0
<i>Oxalis stricta</i> L.	0.01	0	0	0.5	2	0	0
<i>Solanum carolinense</i> L.	0.01	0	0	0.5	2	0	0
<i>Taraxacum officinale</i> Weber	0.01	0	0	0.5	2	0	0
<i>Xanthium strumarium</i> L.	0	0.2	0.2	3.0	0	23	13
<i>Hordeum pusillum</i> Nutt.	0	0.01	0	0.5	0	2	0
<i>Panicum dichotomiflorum</i> Michx.	0	0	0.5	3.0	0	0	48
<i>Eragrostis trichodes</i> (Nutt.) Wood	0	0	0.01	0.5	0	0	3
Average No. species per plot [†]	6.9	6.3	5.1				

* Includes some *I. lacunose* L.

† including *G.max*

Table 4

Correlations (R) and probability (P) of significant environmental vectors with 2-dimensional NMDS ordination of weed species cover data from the natural experiment.

Variable	n	R	P
Time (survey date)	200	0.71	< 0.001
Block	200	0.22	0.006
Soybean biomass (per plant)	196	0.54	< 0.001
Soybean canopy cover	200	0.26	0.001
<i>Setaria faberi</i> density survey 1	131	0.22	0.044
<i>Amaranthus rudis</i> density survey 1	131	0.25	0.035
<i>Amaranthus rudis</i> final density	200	0.26	0.002
<i>Amaranthus rudis</i> standing crop biomass	188	0.25	0.009
Number of species	200	0.65	< 0.001
RWC	119	0.32	0.002
% seed protein time 3	68	0.34	0.045

Figure legends

Fig 1. Three-dimensional nonmetric dimensional scaling ordination of the weed community from the mesocosm experiment. Each circle represents a plot from one of the three surveys.

Fig 2. Species centroids from the 3-dimensional ordination from the mesocosm experiment. Species abbreviations: AMAR = *Ambrosia artemisiifolia*, AMRE = *Amaranthus retroflexus*, AMRU = *Amaranthus rudis*, AMTR = *Ambrosia trifida*, CAPA = *Cardamine parviflora*, CEVU = *Cerastium vulgatum*, CHHU = *Chamaesyce humistrata*, CHAL = *Chenopodium album*, COCA = *Conyza canadensis*, CYES = *Cyperus esculentus*, DISA = *Digitaria sanguinalis*, FEAR = *Festuca arundinacea*, GAAP = *Galium aparine*, IPHE = *Ipomoea hederacea*, LAAM = *Lamium amplexicaule*, MOVE = *Mollugo verticillata*, OXST = *Oxalis stricta*, PALA = *Paspalum leave*, PEPE = *Persicaria pensylvanicum*, PHSU = *Physalis subglabrata*, POAN = *Poa annua*, RAAB = *Ranunculus arbortivus*, SEFE = *Setaria faberi*, SISP = *Sida spinosa*, SOCA = *Solanum carolinense*, SOBI = *Sorghum bicolor* XAST = *Xanthium strumarium*.

Fig 3) Significant vectors associated with the 3-dimensional ordination of the mesocosm experiment. Soy-bio, Soy-can, Soy-d, Soy-fden, Soyscfb, Totyield, Protein, Seedwater, and 100swht = mean individual biomass, canopy cover, density, final density, standing crop final biomass, total seed yield, % seed protein, % seed water, and 100 seed weight, respectively, of *Glycine max*. P_AMRU = sown seed density of *Amaranthus rudis*, P_AMTR = sown seed density of *Ambrosia trifida*, P_SEFA = sown seed density of *Setaria faberi*, AD_Weeds = total density of

sown weeds, No spp = number of species per plot, RWC = soybean relative water content, SFdt1 = *Setaria faberi* density at survey 1, Time = survey date, Even = Simpson's Evenness of target weed canopy cover.

Fig 4) Nonmetric dimensional scaling ordination, 2-dimensional solution of the natural experiment. Each circle represents a plot from one of the three surveys.

Fig 5) Species centroids from the 2-dimensional ordination from the natural experiment. Species abbreviations as in Fig 2 plus: ABTH = *Abutilon theophrastii*, AMAL = *Ampelamus albidus*, ERTR = *Eragrostis trichodes*, HOPU = *Hordeum pusillum*, IPHE = *Ipomoea hederacea/lacunosa*, PADI = *Panicum dichotomiflorum*, TAOF = *Taraxacum officinale*.

Fig 6) Significant vectors associated with the 2-dimensional ordination of the natural experiment. ARd/b represents the average position of 3 vectors associated with the density and biomass of *Amaranthus rudis* (all were aligned between the Block and Soycov vectors), No spp = number of species per plot, RWC = soybean relative water content, Soybio = soybean biomass, Soycov = soybean canopy cover, SFdt1 = *Setaria faberi* density at survey 1, Time = survey date.

Fig 1.

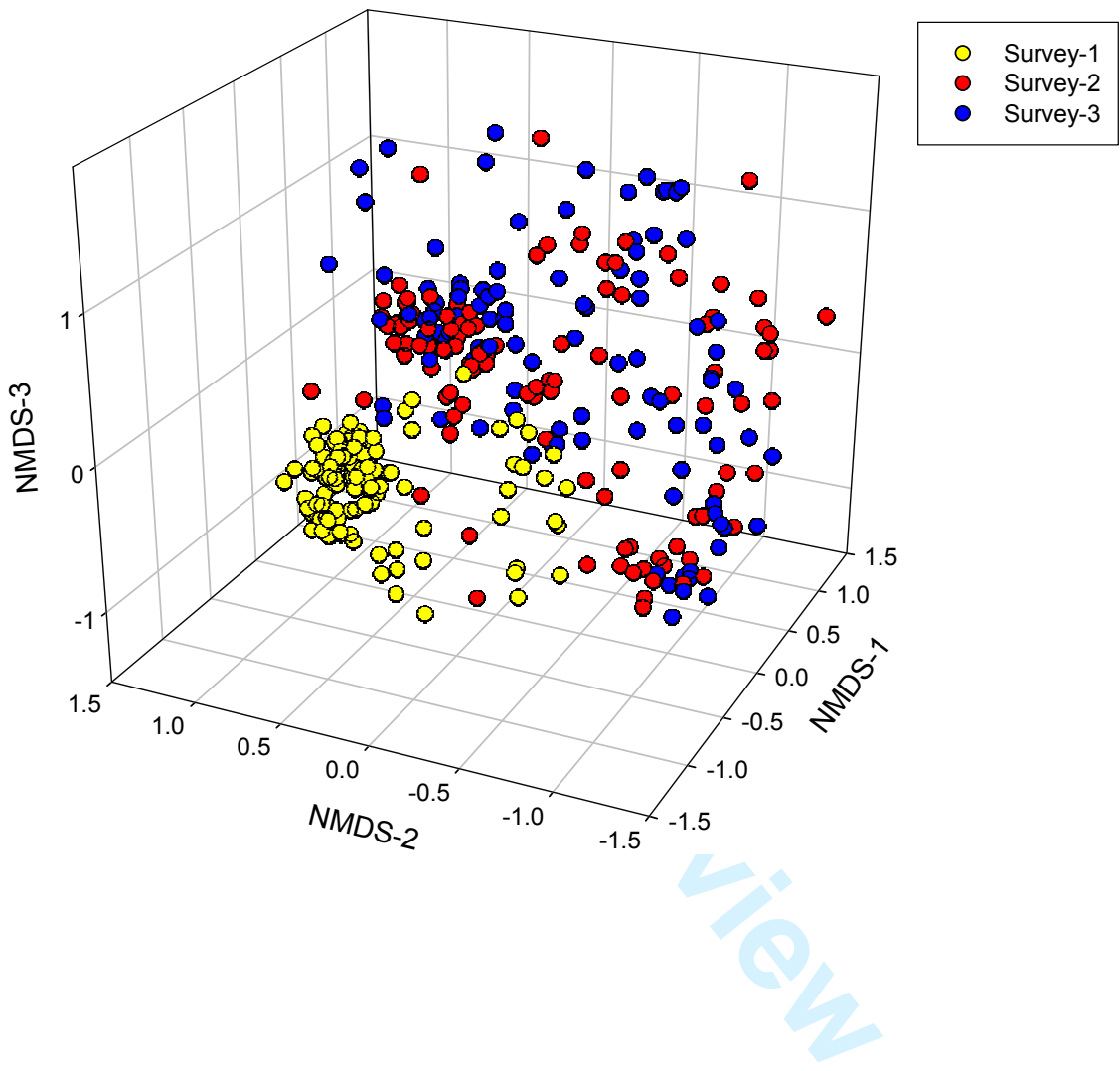


Fig 2.

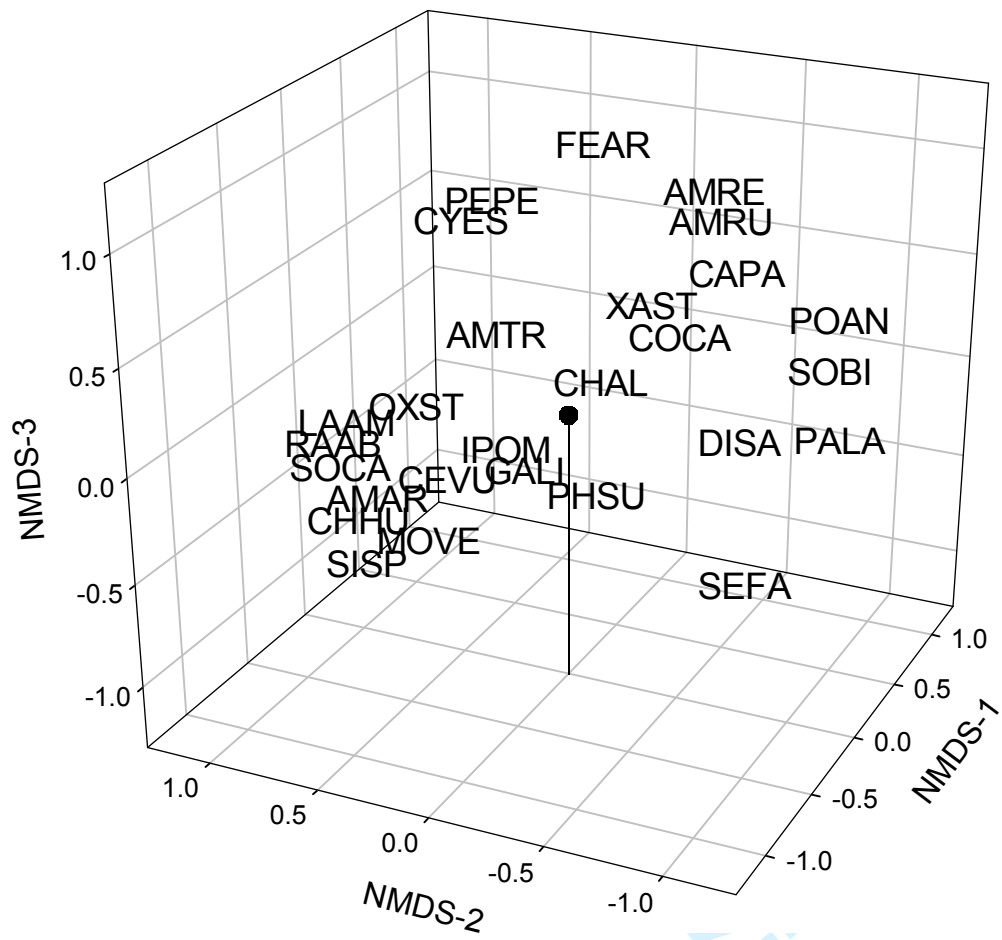


Fig 3)

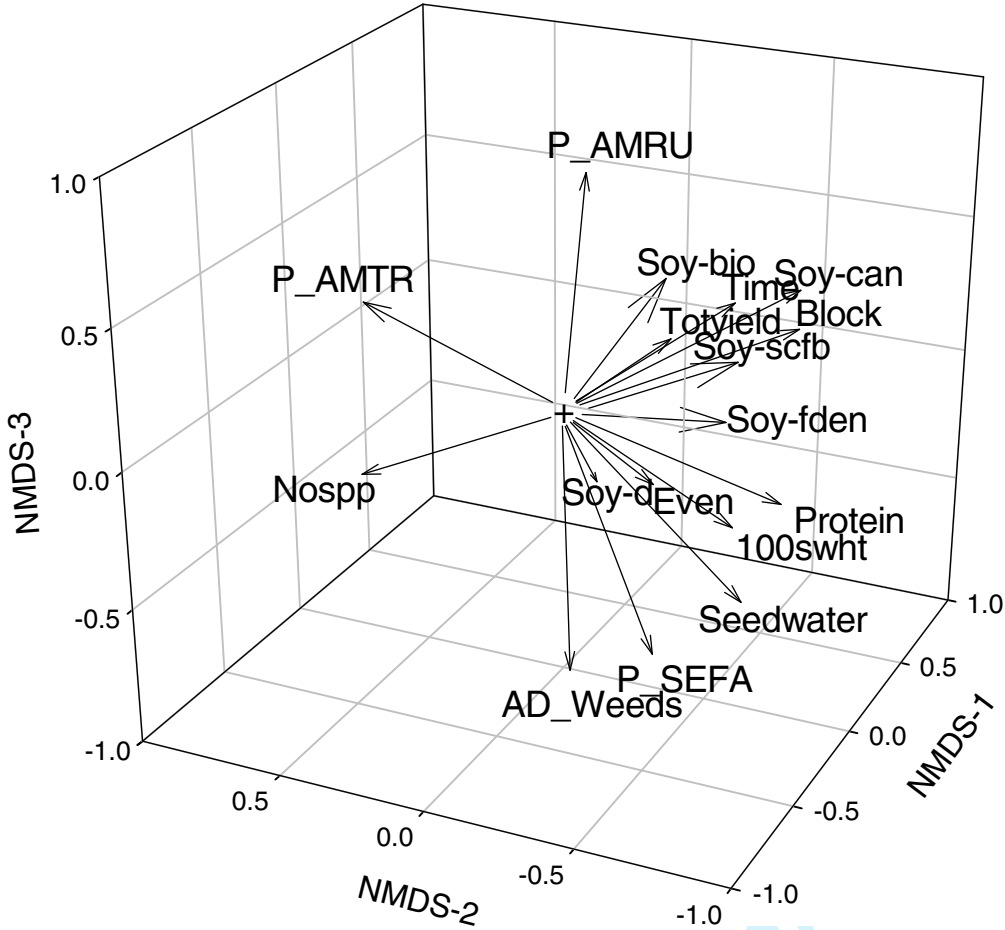
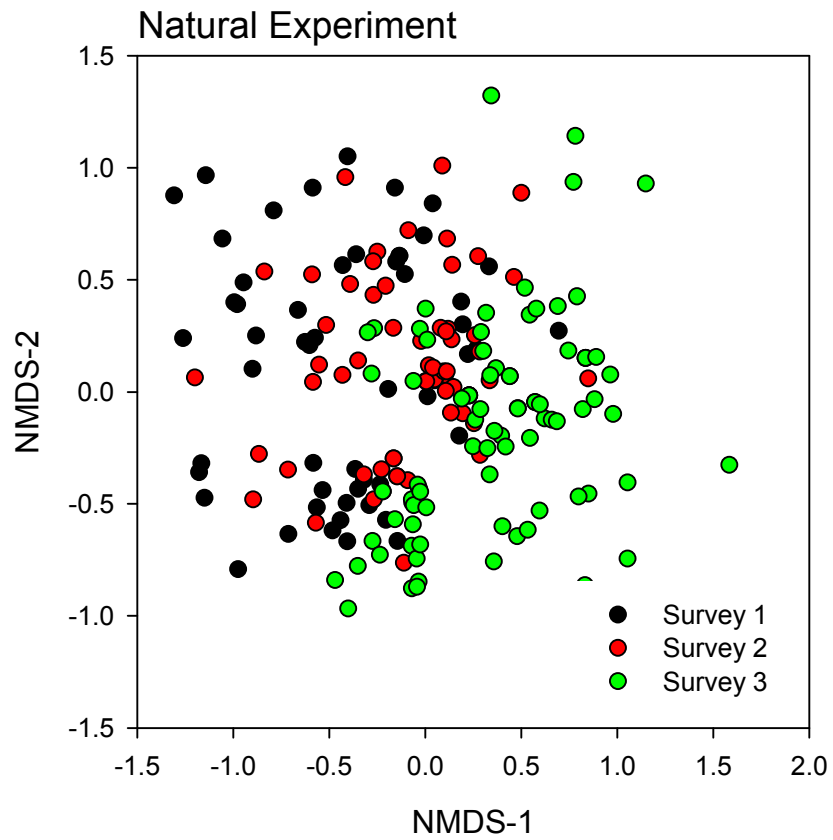
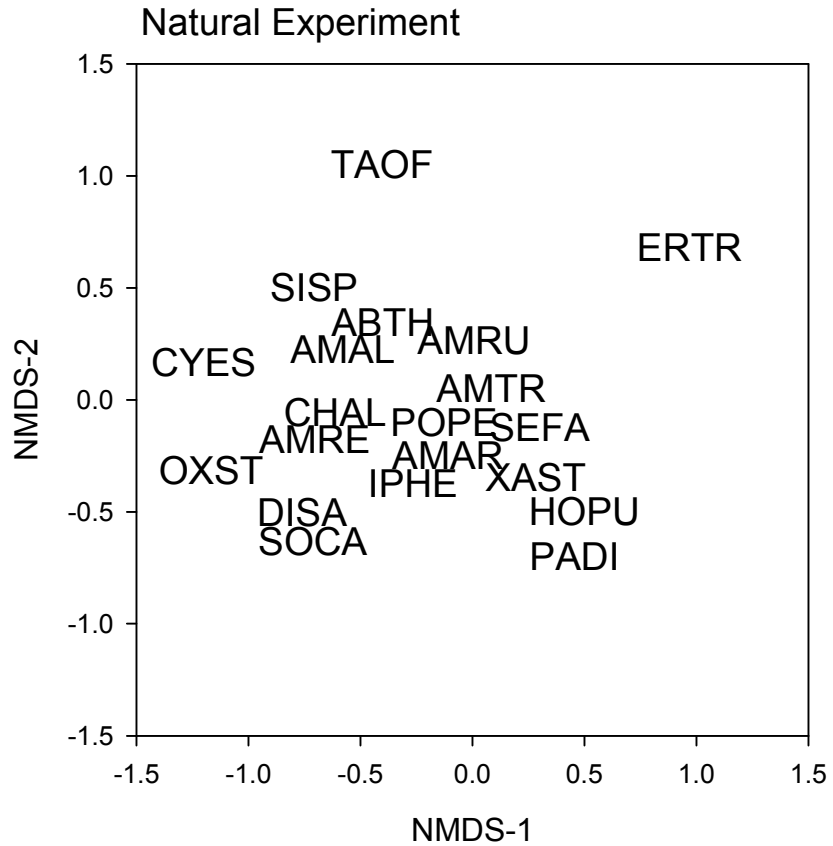


Fig 4)



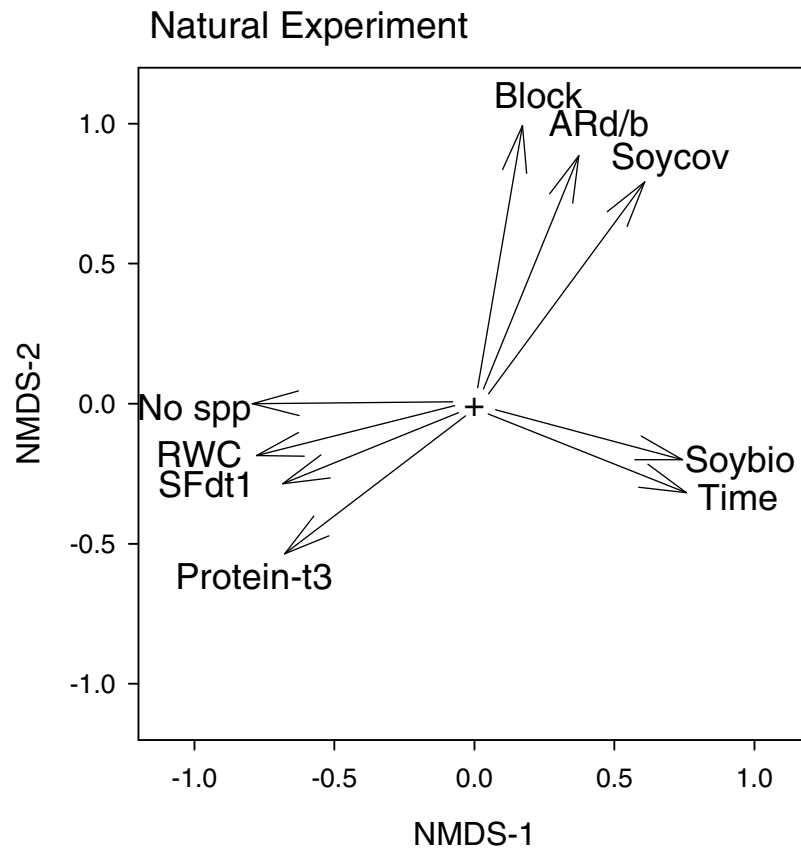
Review

Fig 5)



Review

Fig 6)



Appendix 1. Two-way table of mesocosm plots and species ordered by ascending position (left to right and top to bottom) along the survey 1 protein vector from 3D-NMDS ordination. Species abbreviations as in legend to Fig 2. The data for each species were standardized to unit maxima, and placed into one of four categories; - = absent, 1 = 0.1 – 0.25, 2 = 0.26 – 0.50, 3 = 0.51 – 0.75, 4 = 0.76 – 1.00.

396335865215555111143238147235644188421727364322794191113311519916715292538956996814767144128877182798116167111811111496
116289193105 4700609689218844636 0450395 0 553953338800207378440 071267715390425281217 5710296241006671111 9101 210104 8
3 70 5 42 0 1 1 6 49 3 792 08658

Table with 17 rows (species) and 80 columns (plots). Rows include LAAM, RAAB, SOCA, AMAR, AMTR, IPHU, CHHU, OXST, CAPA, XAST, AMRU, CHAL, AMRE, SISP, POAN, CYES, CEVU, MOVE, SEFA, DISA. Data points are - (absent), 1, 2, 3, or 4.

